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Sea Lamprey – Swedish Action Plan

Petromyzon marinus Linnaeus, 1758

Swedish Agency for Marine and Water Management, report 2020:08

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Preface

Sweden has signed the Convention on Biological Diversity, thereby committing to promoting the protection of ecosystems, natural habitats, and the preservation of viable populations of species. Viable populations are evidence that species have good access to natural habitats, the ability to spread, and that crucial functions and processes in ecosystems are working properly. Approximately five percent of Sweden's animal and plant species lack these conditions and are threatened with extinction. Extraordinary efforts are required to safeguard the most threatened species.

Action plans for threatened species is an initiative focused on species whose existence cannot be ensured through current efforts for sustainable land and water use or existing site protection. These action plans are important tools for the Swedish Agency for Marine and Water Management and the county administrative boards in their efforts to achieve the parliament-decided environmental quality objective “A Rich Diversity of Plant and Animal Life”, as well as the other six ecosystem-related environmental quality objectives.

The Action plan for the sea lamprey (*Petromyzon marinus* Linnaeus, 1758) outlines the Swedish Agency for Marine and Water Management's perspective on conservation goals, and the actions that need to be taken for the species. The program is commissioned by the Swedish Agency for Marine and Water Management, and has been prepared by Nils Ljunggren and Micael Söderman, of the Swedish Anglers Association.

The action program includes a brief overview of present knowledge, together with a presentation of urgent measures for the period 2020-2024 needed to improve the conservation status of the sea lamprey in Sweden. These measures are coordinated among stakeholders, resulting in increased knowledge and understanding of the species and its habitats. The actions have been agreed through consultations and an extensive referral process, allowing governmental authorities, municipalities, experts, and interest organisations to contribute to the program's content.

The action program is an important step towards improving conservation efforts for, and expanding knowledge about, the sea lamprey. The Swedish Agency for Marine and Water Management hopes that the program will stimulate engagement and tangible actions at both regional and local levels, allowing the species to eventually achieve a favourable conservation status. The Swedish Agency for Marine and Water Management extends gratitude to all those who provided input in the development of the action program, and to those who will contribute to its implementation.

Gothenburg, January 2020,

Mats Svensson

Head of the Department of Marine and Water Management

Approval, Validity, Evaluation, and Availability

The Swedish Agency for Marine and Water Management decided on January 27, 2020 (Reference Number 3207-18), to approve the action plan for sea lamprey.

The plan is a guiding, non-formally binding document, applicable during the years 2020-2024. Evaluation and necessary revision will take place during the final year of this period. If needed, the action plan may be evaluated and revised earlier.

This and other action programs can be downloaded from www.havochvatten.se

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Summary

The sea lamprey has, like other diadromous species, high environmental requirements. In addition to free migration routes, the sea lamprey needs high structural complexity in the watercourse, with rapids, calm hollows and dead wood. The species is highly dependent on larger fish to prey on during its marine, parasitic phase, and is therefore in need of healthy fish populations at sea. All in all, the sea lamprey is a valuable umbrella species for a large number of species with similar environmental requirements. Atlantic salmon, eel and river lamprey are examples of other migrating fish species that benefit from actions proposed in this action plan.

Inventories have been conducted in all counties along the Swedish west coast from north-western Skåne to the Norwegian border. Sea lampreys were only found in waterways with presence of salmon, confirming that the two species to a large degree share requirements on spawning habitats.

Our knowledge about sea lamprey presence in freshwater is more limited in the counties Västra Götaland and Skåne as compared to the county of Halland, and additional inventories are needed for a more complete picture of sea lamprey presence and population status in Sweden.

Hydroelectric plants and other obstacles blocking migration routes are considered a main reason for the decline of sea lamprey numbers. In cases were fish passage solutions exist they are most commonly designed for salmonids, and formed as pool-and-weir fishways where fish have to jump from one pool to another against the current. This type of fish passage solutions cannot be passed by the sea lamprey or other species lacking the ability to pass vertical barriers.

In addition to creating migration barriers, the production of hydroelectric power may cause fast and unnatural fluctuations in flow and hydrological conditions, risking to either lay dry or flush the sediment banks needed by sea lamprey larvae. Several generations of larvae can thus be influenced by a single event. Furthermore, dam construction often transforms riverbeds necessary as spawning and as nursery habitats to lake-like environments.

Lack of large hosts in the sea is assumed to be a major negative factor affecting sea lamprey growth and survival. This may be critical especially during the later part of the growth period, forcing sea lampreys to switch host more often, potentially resulting in a negative energy balance.

There is no evidence that sea lampreys are homing to their natal river for spawning. Instead, individuals which are ready to spawn migrate upstream attracted by chemical cues released by sea lamprey larvae. Consequently,

regular exchange of individuals between rivers is to be expected and local conservation measures, for example the restoration of larval habitats, could potentially attract spawners from large areas. In contrast to salmon, which have unique river stocks, there is less need to consider local adaptations when attempting to re-introduce sea lamprey.

The re-creation of free migration routes to spawning grounds and nursery areas is the most important measure to strengthen the Swedish population of sea lamprey. However, such measures may affect ongoing water regulations, and therefore require coordination with water management and enforcement.

Other actions proposed in this plan are measures to re-create and improve spawning grounds and nursery areas together with protection of the species' habitats. In addition, reinforcement of small populations and re-introduction in areas where the species has disappeared may be needed.

Activities to improve knowledge of the sea lamprey's environmental needs, and information efforts aimed at authorities, fishermen, landowners and the public are proposed.

Species Facts

Species description and identification

There are three species of lampreys in Sweden: sea lamprey (*Petromyzon marinus*), river lamprey (*Lampetra fluviatilis*), and brook lamprey (*Lampetra planeri*). The sea lamprey is the largest and rarest among these species.

Lampreys – general description

At first glance, a lamprey can be mistaken for an eel, but lampreys have several characteristics that set them apart from true fish. The most obvious is the peculiar mouth. Instead of jaws, adult lampreys have a circular sucking disc with which they can attach themselves to host animals or solid objects. The sucking disc is surrounded by small fringes, *fimbriae*, which help it seal completely around its edges. The inside of the sucking disc, like the tongue, is filled with small sharp keratin-covered teeth used to scrape and bore through the skin of their host. The placement and shapes of these teeth are important features for species identification and classification of lampreys. Species with many and undifferentiated teeth are considered more ancient (Holčík, 1986).

Figure 1. The openings of a sea lamprey's gill sacs are visible as a row of seven small holes behind each eye. In front of the eyes is a single nostril. The photo depicts a male from river Rolfsån, Halland. Photo: Nils Ljunggren.

Lampreys have well-developed dorsal and ventral fins, but they lack paired pectoral and pelvic fins. The skin is smooth, without scales, and covered in mucus. The openings of the gill sacs are seen as a row of seven small holes behind each eye. In front of the eyes is a single nostril (Figure 1).

Sea lamprey – description

The sea lamprey, *Petromyzon marinus*, is the largest of the currently living lamprey species, with a maximum length of 120 cm and a weight of 2.3 kg (Holčík, 1986). The species is robustly built, and easily recognisable in its adult stage by its marbled body sides in shades of brown, red, and grey (Figure 2). The typical length of spawning individuals in the British Isles ranges from 60 to 90 cm (Kelly & King, 2001), which aligns well with Swedish observations (Söderman & Ljunggren, 2009). There is a tendency for increased average length of spawning individuals the further south you go in Europe (Beaulaton, 2008).

Figure 2. The sea lamprey is strongly built, and sexually mature individuals are easily recognised by their marbled body sides in shades of brown, red and grey. The photo shows a male with the characteristic finger-thick formation along the back. Photo: Nils Ljunggren.

Secondary sexual characteristics

The lamprey species found in Sweden share several secondary sexual characteristics that become apparent during the spawning period (Figure 3). Common to both sexes is a reduction in the distance between the rear and front dorsal fins. In females, additional features include a swollen cloaca, thickened rear dorsal fin, and an anal fin-like formation behind the cloaca. Males develop a genital papilla measuring just over 5 mm. Particularly distinctive for the sea lamprey is that males, in preparation for spawning, develop a finger-thick ridge along the upper side of the back (Figure 2).

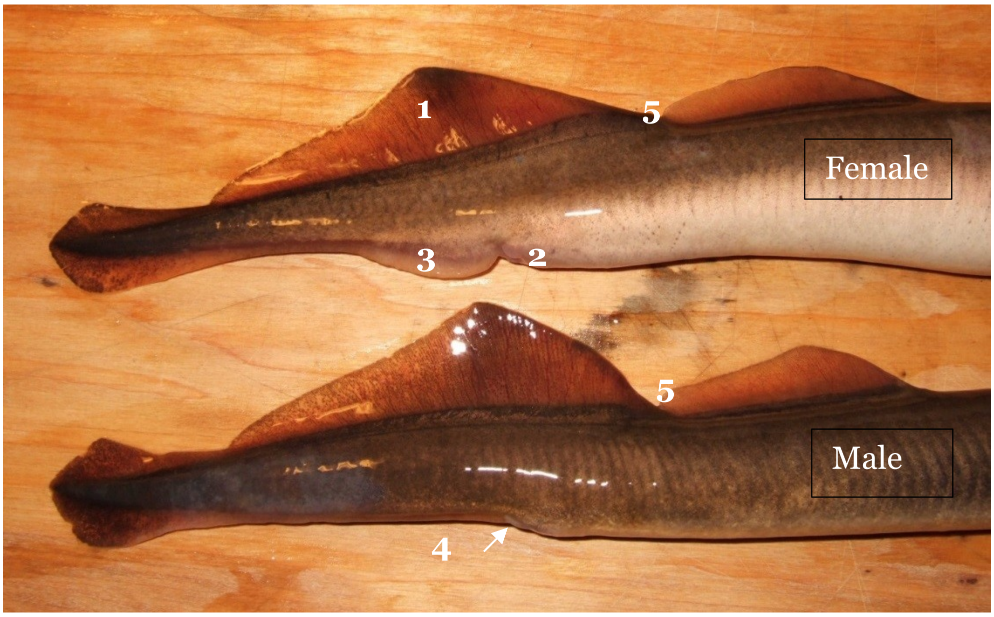

Figure 3. The lamprey species found in Sweden share several secondary sexual characteristics. The photo shows a female (top) and male river lamprey. The female is recognised by a thick and fleshy rear dorsal fin (1), a swollen cloaca (2), and a anal fin-like projection behind the cloaca (3). The male develops a genital papilla (4). In both sexes, the space between the front and rear dorsal fins disappears (5). Photo: Nils Ljunggren.

Young, recently metamorphosed sea lampreys have a silver-coloured belly and darker blue-black sides and back. This colouration is typical for a species living in the open waters of the sea, providing effective camouflage. The mouth, which in young individuals can constitute over 8% of the total body length, is internally entirely covered by approximately 150 relatively uniform, keratinised teeth arranged in rows (Gardiner, 2003). The well-developed scraping tongue also has sharp teeth (Figure 4).

Figure 4. The sea lamprey's mouth and tongue, with its approximately 150 keratinised teeth, is an impressive sight. Photo: Nils Ljunggren

Larvae

Whilst adult sea lampreys during their spawning migration are relatively easy to both detect and to identify, the opposite is true for the species' larval stage (Figure 5, 6). The morphological differences between lamprey larvae and adults are so significant that it wasn't that it was understood they belong to the same species until the 1850s. Occasionally, the old scientific name for lamprey larvae, *Ammocoetes branchialis*, is used even in relatively modern literature (Hardisty, 2006).

The external mouthparts of lamprey larvae consist of lobed lips adapted for filter feeding, distinctly different from the adult lamprey's sucking disc (Figure 6, 7). Teeth are absent since the larvae live as filter feeders burrowed in the river bed, and their eyes, still poorly developed, are hidden beneath the skin, only hinted at as a darker shading.

Figure 5. Larvae of river, brook, and sea lampreys together with young trout from river Kungsbackaån. The depicted larvae are all relatively large and will, within 1-2 years, begin their metamorphosis into fully developed lampreys. Photo: Micael Söderman.

Figure 6. The external mouthparts of lamprey larvae consist of lobed lips adapted for filter feeding, distinctly different from the adult lamprey's sucking disc. The photo shows a larva of the sea lamprey with characteristic darkly pigmented mouthparts; compare with the larva of the river/brook lamprey in Figure 7. Photo: Micael Söderman.

Figure 7. Front part of river/brook lamprey. As larvae these species are indistinguishable. However, they differ from sea lamprey larvae by lacking pigmentation on the lobed lips, and different pigmentation pattern on the tail. Photo: Nils Ljunggren.

Lamprey larvae grow slowly, and after one year, the larvae of all species found in Sweden are only 20 to 40 mm long. Annual growth then ranges from 20 to 40 millimetres per year, depending on temperature and food quality (Hardisty & Potter, 1971; Holčík, 1986). Most European and North American sea-migrating sea lampreys undergo metamorphosis before reaching a length of 155 mm at the age of 5 years (Hardisty, 2006) (Figure 8).

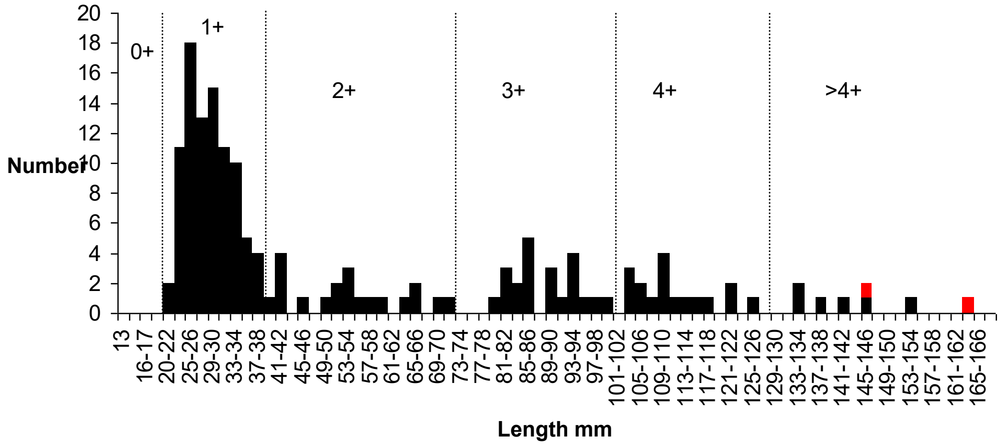

Figure 8. Length distribution for 156 sea lamprey larvae caught during electrofishing in Halland in 2008. Red bars indicate larvae with initiated metamorphosis. No consideration has been given to potential growth differences between different populations. Vertical dashed lines indicate estimated classification into age groups (number of years + time from hatching) from year-old larvae (0+) up to larvae with an age over four years (>4+).

Tracks and signs

The spawning nests – redds – consist of meter-sized depressions in the bottom substrate (Figure 9), making them identifiable even long after the spawning has concluded, especially with some experience of looking for the signs. Although, at first glance, these spawning nests might be confused with those of salmon or large sea trout, no other organisms in Swedish waters sort the bottom substrate in the same way. Any potential confusion should instead involve structures created by humans.

Figure 9. The meter-sized spawning nests created by the sea lamprey by moving stones up to 15 centimetres in diameter are easy to identify. On the left side of the photograph, a male is seen attached to a large stone at the front of the spawning nest, which has been cleared of cobbles and stones. Photo: Nils Ljunggren.

The sea lamprey attacks a broad spectrum of species during its parasitic phase (Silva *et al.*, 2014), and larger prey typically survive the attack. Both on dead and surviving hosts the attack leaves characteristic circular scars with a smaller central wound from the lamprey's gnawing tongue (Figure 10).

Figure 10. Juvenile sea lamprey attached to a cod. Despite the attack, the cod has bitten onto a baited hook. Directly after metamorphosis sea lampreys are shiny silver, but with age, the juveniles become increasingly blue and black speckled. Compare with the more brown, red and grey colouring of individuals that have returned to freshwater for spawning (Figure 1, 2, 9). Photo: Markus Lundgren.

Subspecies and varieties

There are no identified subspecies or taxonomic varieties. In Europe the sea lamprey feeds almost exclusively at sea. Feeding sea lampreys have been found in a small number of lakes in Ireland, however it has not been established if they are able to complete their life cycle in freshwater (King & O'Gorman, 2018)[1]. A small lake-dwelling form naturally inhabits several lakes along the East Coast of North America. After the opening of the fourth Welland Canal in 1932, sea lamprey invaded North America's Great Lakes system, causing large damage to the original fish fauna and local fisheries.

Similar species

The two genera of lampreys found in Sweden, *Petromyzon* and *Lampetra*, have larvae that may appear similar at first glance. However, differences exist, particularly in the pigmentation of the external mouthparts and the tail fin. Sea lamprey larvae exhibit widespread dark pigmentation in these features (Figure 6, 7, 11).

Figure 11. The larvae of the sea lamprey (genus *Petromyzon*) and river/brook lamprey (genus *Lampetra*) are easy to distinguish by the pigmentation on their tails. In the sea lamprey, the pigmentation extends into the tail fin (upper individual), while in the river/brook lamprey, it is limited to the the body itself (lower individual). Photo: Micael Söderman.

Fully grown sea lampreys can be distinguished from the other two lamprey species found in Sweden based on several characteristics, including differences in body size, pigmentation, and the appearance and placement of the teeth.

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[1] Information updated and added in the English language version.

The river lamprey and brook lamprey are two closely related and morphologically very similar species, with the brook lamprey evolving as a non-parasitic sibling species to the river lamprey. Fully-grown river lampreys typically reach a length between 25 and 40 cm and a weight around 50 g (Holčík, 1986; Maitland, 2003; Ljunggren, 2007). Brook lampreys rarely exceed 15 cm in length, but a few individuals can reach up to 17 cm, and they weigh only 6-7 g (Holčík, 1986; Maitland, 2003). When newly metamorphosed, river lampreys have silvery body sides with a dark back and a light or faintly marbled belly. However, they darken during spawning migration, and become darkly coloured in shades of grey, brown, and green during spawning. Brook lampreys are silver coloured for a short period after metamorphosis in late summer and autumn, but they darken soon after and, during spawning, have the same appearance as river lampreys in pattern and colour (Figure 12; Maitland, 2003; Gardiner, 2003).

Figure 12. Fully developed brook lamprey. River lamprey and brook lamprey, when mature and ready to spawn, look very similar with a light, sometimes faintly marbled, belly and back, and body sides in shades of brown, grey, and green. The significant difference in size usually makes the two species easy to distinguish as adults. Brook lamprey is barely thicker than a pen and rarely exceeds 15 cm in length, while river lamprey is as thick as a finger and can reach 40 cm in length. Photo: Nils Ljunggren.

Conservation genetics

Genetic variation

Genetic studies of sea lampreys from Western Europe indicate a relatively low degree of genetic differentiation (Almada *et al.*, 2008; Pereira & Almada, 2013). Studies have not been able to confirm any homing behaviour (the species returning to its natal stream to spawn) in lampreys. This, combined with the sea lamprey's long marine migrations, probably hinders the emergence of genetic differences between different watercourses and regions (Goodman *et al.*, 2008; Waldman *et al.*, 2008).

Analyses of mitochondrial DNA show that populations in North America exhibit considerably more haplotypes, and a comparison with sea lampreys from Europe suggests that the species migrated into Europe from North America approximately 300,000 years ago (Pereira & Almada, 2013). Analyses of sea lampreys caught off the coast of Iceland indicate a high likelihood of European origin (Pereira *et al.*, 2012).

Genner *et al.* (2012) conclude that local conservation measures, such as providing access to new larval habitats, can have positive effects on the abundance of spawning sea lampreys across large areas. At the same time, they note that in conservation efforts targeting sea lampreys, there is no need to worry about various local adaptations in the same way as with salmonid fishes, where reintroduction can be complicated after local stocks have been wiped out.

That there may be differences between populations is demonstrated by Lança *et al.* (2014), who found morphological and physiological differences when comparing sea lampreys from three topographically separate marine areas along the Portuguese coast. Sea lampreys from different river systems were largely confined to the adjacent marine area due to sea bed morphology. This was interpreted as local adaptations to both spawning rivers and the marine environment.

Genetic issues

The anadromous nature of lampreys, coupled with the absence of a proper homing behaviour, most likely results in a relatively large genetic exchange between different watercourses (Goodman *et al.*, 2008). Even Swedish watercourses with a limited presence of spawning sea lampreys should thus experience a recurrent influx of sea lampreys from both nearby waters and more distant regions. If nothing indicates the opposite, the risk of genetic depletion in spawning populations in watercourses with few spawning fish is considered to be low.

Biology and ecology

Lifecycle

Lampreys have a largely unique life cycle with two distinct and separate life stages where appearance, physiology, and habitat differ. In brief, the sea lamprey life cycle consists of a larval period lasting 5 to 7 years, including metamorphosis, and a period of up to 3 years as a free-swimming parasite. After spawning, the lampreys die (Figure 13).

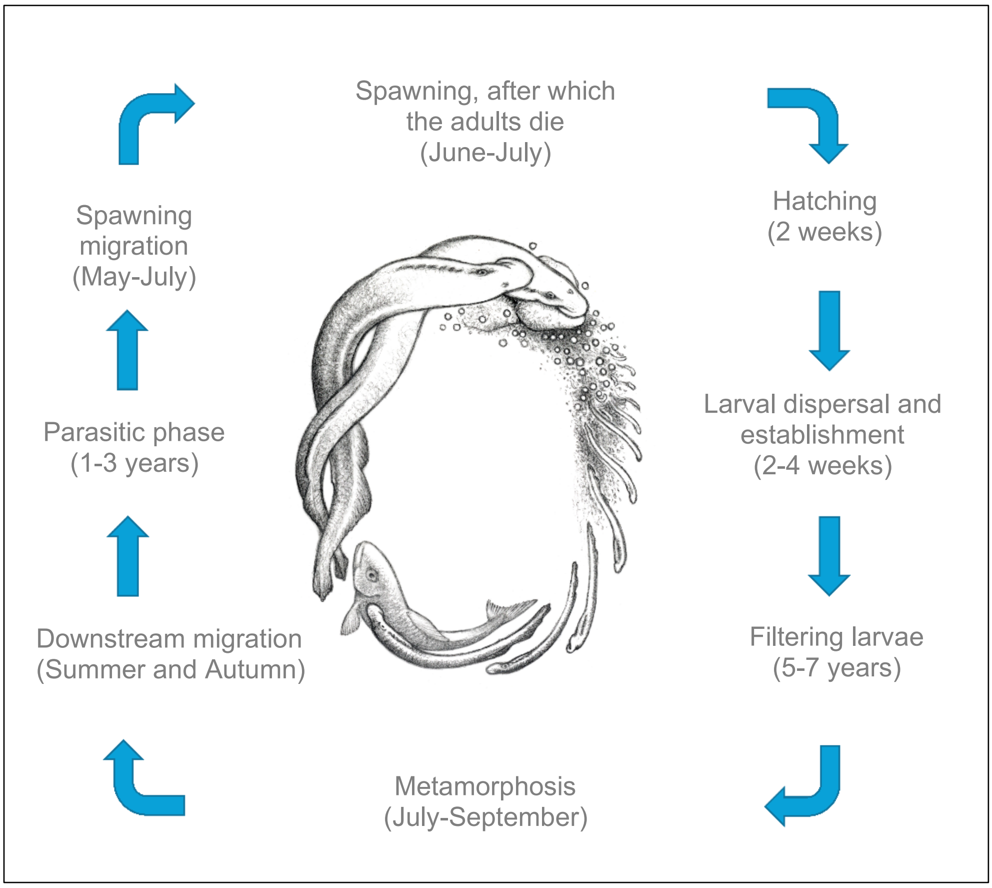

Figure 13. Like other parasitic lamprey species, the sea lamprey has a complex life cycle where different life stages have greatly different demands on its habitat. Illustration by Linda Nyman, Swedish Species Information Centre.

Reproduction and dispersal

Spawning

Spawning commences when the water temperature rises above 15 °C, usually in June, certain years from the end of May, or not until July (Maitland, 2003; Holčík, 1986; Söderman & Ljunggren, 2009; Åberg & Thorsson, 2010). Typically nocturnal, sea lampreys change to a very bold behaviour with activity around the clock. It is not uncommon for spawning to occur in direct sunlight (Holčík, 1986; Söderman & Ljunggren, 2009).

Spawning usually occurs in pairs. The construction of the redd is initiated by the male, and defending the redd can result in violent disputes between males. The males release a pheromone that is strongly attractive to females (Wagner *et al.*, 2006), and as soon as the females join the spawning sites, they participate in redd-building.

The male pheromones have long been utilised by fishermen in French rivers. By keeping mature males in fish traps, they significantly increase the number of captured females in the same trap. The effect has been further validated through field tests on sea lampreys in the Great Lakes (Wagner *et al.*, 2006). In addition, females emit substances that attract males (Sorensen & Hoyle, 2007).

The spawning sites are usually located on top of riffles, and therefore relatively easy to locate (Hardisty 2006; Söderman & Ljunggren 2009). Using their mouths and the force of the water, the sea lamprey move stones until a redd is formed in the river bed. If the current is not too strong, stones of up to 15 cm in size are placed both upstream and downstream of the red, otherwise, all stones are placed downstream. In stronger currents, significantly larger stones and smaller blocks may be dragged out of the redd for deposition downstream (Figure 9, 14, 15).

Figure 14. Adult male sea lamprey attaching to a small size stone. Using its body as a lever it is able to move large stones in order to form a redd. Photo: Nils Ljunggren.

The size of the redds generally corresponds to the body length of the sea lamprey. The median length for 161 redds in watercourses in Halland was measured at 1 m (mean value 94 cm). The median width of the nests was 1 m (mean value 143 cm). However, the redds can be significantly wider in cases where several individuals collaborate or multiple redds merge. The water depth immediately upstream of 26 active redds ranged from 25 to 65 cm (mean value 51 cm). Most nests had a typically elongated elliptical appearance with the long side at right angles to the direction of the current (Söderman & Ljunggren, 2009).

Figure 15. With the help of the water, sea lampreys can drag away stones up to the size of a brick. Photo: Micael Söderman.

During the mating act, the female attaches herself to a stone at the front of the redd. The male, in turn, attaches himself to the female's head and wraps his tail around her. As the pair begins to vibrate vigorously, the male pushes his tail backward against the female's cloaca, thus squeezing out a portion of the sticky and approximately 1 mm sized eggs. The shaking of the pair stirs up sand to which the sticky eggs adhere and sink to the river bed where they are buried (Figure 16, 17) (Hardisty 2006; Söderman & Ljunggren, 2009). It has been estimated that a female lays an average of 172,000 eggs (Hardisty, 2006). Studies on sea lampreys in North America revealed that around 80% of the eggs were swept downstream during spawning, and only about 10% of the eggs survived to hatch (Hardisty, 2006).

The time from fertilization to hatching is approximately 2 weeks. At hatching the larvae are between 4 and 7 mm long (Holčík, 1986; Maitland, 2003). The development from egg to viable larva in sea lampreys has been shown to occur within a temperature range of 15 to 25 °C.

Figure 16. Spawning sea lampreys. The sticky eggs adhere to the stirred-up sand and are then buried at the bottom of the redd. Photo: Nils Ljunggren.

Larval stage

The larvae leave the redd within three weeks after hatching. They move into open water and drift downstream to a suitable habitat, where they burrow into the riverbed. They prefer fine-grained sediments such as sand, silt, and organic debris (Holčík, 1986). Even areas with fine-threaded, waterlogged roots can be used as a habitat during the growth phase (O'Connor, 2004; Ljunggren & Söderman, 2009).

Lamprey larvae were formerly popularly referred to as linål in Swedish ("flax eel"), a name derived from the fact that they were often found in flax laid in watercourses for retting (Svanberg, 2000).

Figure 17. The yellowish-white sticky eggs of the sea lamprey adhere to the churned-up sand during spawning and sink to the bottom of the redd. Photo: Nils Ljunggren.

In slow-flowing streams with good nursery areas, the larvae may remain within the same area until metamorphosis. However, in rivers with larger gradients and higher stream velocities, there is a gradual downstream migration of larvae, and larger larvae are generally found farther away from the spawning grounds. Passive transport during periods of high water flows, or active movement during periods of extreme low flows, are important factors in their dispersal.

Lamprey larvae feed on fine detritus, algae, and bacteria filtered from the flowing water and the upper sediment layer. Their food also includes protozoa, nematodes, and rotifers (Kelly & King, 2001). Food particles are captured by mucus in the larva's pharynx, gathered into clumps, and then swallowed (Hardisty, 2006). The relatively sedentary life of lamprey larvae, coupled with a low metabolism, enables them to withstand the low oxygen levels often present in the sediment. However, excessive amounts of decaying organic material in stagnant water can reduce oxygen levels to the point where larvae are compelled to seek new areas (Maitland, 2003; Hardisty, 2006).

Metamorphosis and migration to the sea

Metamorphosis from larva to fully developed lamprey begins during the summer, and is often highly synchronised within a watercourse. Temperature is believed to be the most crucial inducing environmental factor (Holčík, 1986).

The most obvious external changes during metamorphosis are the development of the previously undeveloped eyes and the transformation of the larval filtering apparatus into the characteristic oral disc of the adult lamprey (Figure 18, 19). The body sides become silver-coloured, and the gill apparatus adapts to function even when the lamprey is attached to its host or a rock (Hardisty, 2006). Metamorphosed lampreys move to areas with coarser particles, probably to avoid damage to the altered gill system (Kelly & King, 2001).

Examples of internal changes include changes in osmoregulatory capacity as an adaptation to life in a marine environment, the development of salivary glands, and the degeneration and transformation of the kidneys to cope with the new diet. While much of the external changes are completed in just 4 to 5 weeks, the extensive internal changes mean that it takes up to 8 months for metamorphosis to be complete (Hardisty, 2006).

Juvenile sea lampreys migrate downstream to the sea during late autumn and until mid-winter. Migration occurs at night, is induced by high water flow, and is often strongly synchronised within individual watercourses (Kelly & King, 2001). In studies conducted in the River Severn in the UK over two weeks, almost the entire catch of 400 emigrating sea lampreys was concentrated in a single night (Hardisty, 2006).

Figure 18. Sea lamprey from river Fylleån in Halland, captured during electrofishing in August. The 165 mm transformer has initiated metamorphosis, and the previously concealed eyes are becoming more distinct. Photo: Nils Ljunggren.

Figure 19. The disproportionately large eyes in newly metamorphosed lampreys are the reason why they sometimes are being called *macropthalmia*. The image shows a river or brook lamprey with completed external metamorphosis. Photo: Nils Ljunggren

Feeding and adult migrations

In common with other parasitic lampreys, sea lampreys initiate feeding by attaching themselves to their host with their oral disc. By scraping with their teeth and tongue, they work their way through the skin and begin feeding on blood. As in many blood-sucking animals, lamprey saliva contains substances that dissolve tissues and prevents the blood of the host animal from coagulating. Therefore, a significant part of digestion occurs outside the lamprey. Tissues are effectively consumed in liquid form (Hardisty, 2006).

Different species of lampreys employ different feeding strategies. Unlike, for example, the river lamprey, which consumes both tissues and blood, the sea lamprey primarily feeds on blood. Because blood is relatively nutrient-poor, and fish have low blood content, relatively large fish are required for the energy investment in the attack to be worthwhile. The ideal situation is that the host animal continuously produces new blood in pace with what is lost. It has been estimated that, to maintain a neutral blood balance, the host animal should be 40 times larger than the parasitic lamprey (Hardisty, 2006). For a fully grown sea lamprey weighing 1 to 2 kg, this would mean hosts with weights of 40 to 80 kg.

Catches of, on average, 182 (155–218) mm long, fully developed juvenile sea lampreys in the French Loire and English Severn at the end of December (Hardisty, 2006) and discoveries of both scars and attached, feeding individuals on freshwater fish in Irish water systems, show that sea lampreys may begin their parasitic phase in freshwater whilst migrating to the sea (Silva *et al.*, 2014). The juvenile sea lampreys grow rapidly, and based on studies of freshwater sea lampreys in North America, it is believed that the parasitic phase of the Atlantic Sea lamprey typically lasts for 23 to 28 months (Hardisty, 2006).

Knowledge of the sea lamprey's prey choice during its time in the sea is based on findings and scars on a wide range of fish species, including sprat, herring, sturgeons, salmon, cod, haddock, whiting, pollack, hake, basking shark, and swordfish. Marine mammals are also preyed upon and scars from sea lampreys have been found on grey whales, blue whales, sperm whales, porpoises, and beaked whales (Maitland, 2003; Hardisty, 2006). In total there is documentation of sea lampreys preying upon 54 species of fish and marine mammals (Silva *et al.*, 2014).

The range of host species suggests that sea lampreys usually stay relatively close to the coast, but some individuals actively or passively migrate over large areas and at great depths. The various species and sizes of host organisms likely play different roles as sea lampreys grow.

The large fish and marine mammals required for a fully grown sea lamprey to optimize its nutrient intake often live far out in the ocean. Therefore, it is not surprising that sea lampreys have been found whilst deep-sea trawling at depths of up to over 4000 meters and 650 kilometres from the nearest coast (Kelly & King, 2001; Hardisty, 2006). The fact that many of the host species are among the real long-distance travellers of the oceans probably contributes to the sea lamprey's widespread distribution during its time in the sea. Free living sea lampreys in the waters around Iceland, far from the nearest spawning area, have been genetically traced back to the European population (Pereira *et al.*, 2012).

Spawning migration

When sexual maturity occurs the adult sea lampreys move up into rivers where the scent of larvae indicates the presence of suitable spawning and nursery environments. This behaviour is considered an adaptation to the extensive and unpredictable geographical distribution associated with life as a parasite on large, long distance travelling fish and marine mammals (Goodman *et al.*, 2008; Waldman *et al.*, 2008; Silva *et al.*, 2014; Pereira *et al.*, 2012; Spice *et al.*, 2012).

Once the control of lamprey larvae around the Great Lakes in North America began in the late 1950s it was soon observed that rivers where the larvae had been eradicated immediately had lower attraction for spawning adult lampreys (Hardisty, 2006; Sorensen & Hoyle, 2007). It was suspected early on that some forms of pheromones were involved, but it was not until the 2000s that the active substances could be isolated, and their attractiveness to sexually mature sea lampreys was demonstrated through experiments in both field and laboratory environments (Lance & Sorensen, 2001; Hardisty, 2006; Wagner *et al.*, 2006; Sorensen & Hoyle, 2007).

The migration of sea lampreys up into rivers primarily occurs in direct connection to spawning. Depending on the latitude, this means that migration occurs from December in Southern Europe to June in Northern Europe. Old records suggest that during the medieval period, sea lampreys migrated upstream in the Severn as early as winter, probably because the climate was then warmer and resembled today's Southern European conditions. In Portugal, the migration peak is usually reached at the end of April (Hardisty, 2006; Quintella *et al.*, 2004).

Observations at the Herting Power Station in river Ätran, where migrating sea lampreys were lifted over the dam until 2013, show that sea lampreys attempted to move further upstream in the water system from the end of May until the end of July, with the main part passing in the second half of June (Figure 20; Alenäs, 2013).

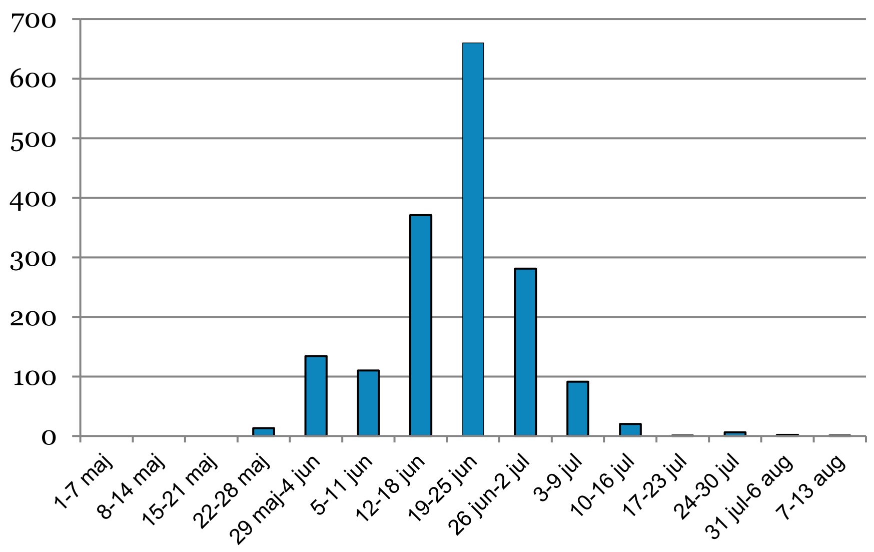

Figure 20. Seasonal occurence of sea lampreys caught and lifted past the dam at the Herting Power Station in river Ätran during the period 2008-2013.

Data from the new fishway in river Ätran in 2014 and 2015 indicate a highly concentrated spawning migration, where most of the migration during a single year was recorded lasting one week. However, the timing of the migration varied significantly between the two years (Figure 21).

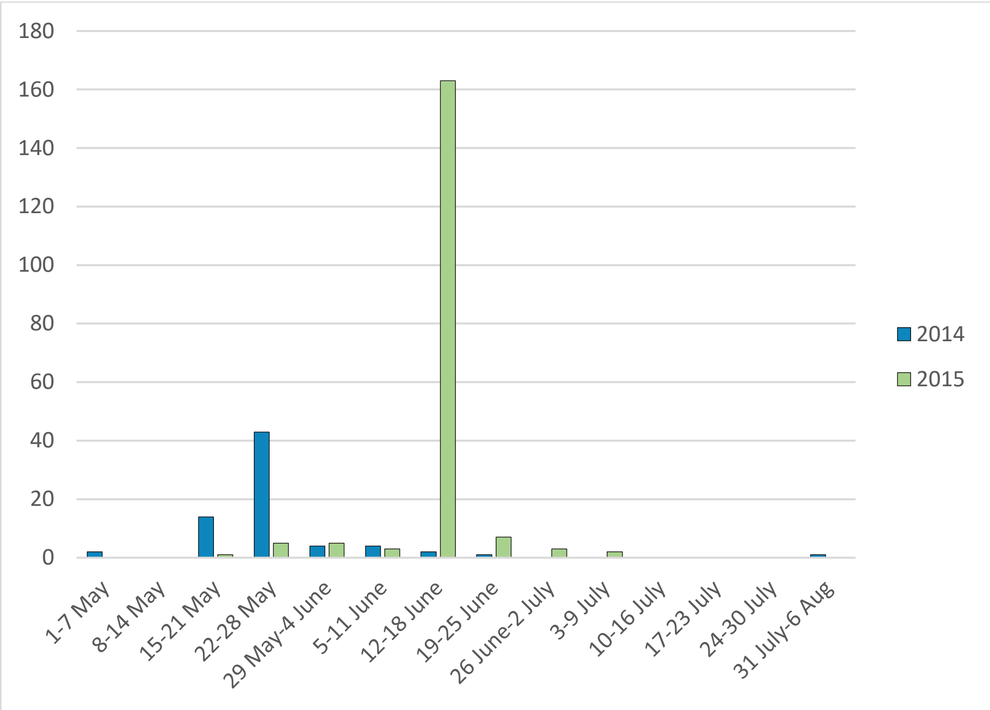

Figure 21. The number of migrating sea lampreys recorded in the fish counter at Herting in river Ätran during 2014 and 2015. The diagram shows a very concentrated migration, whilst the timing of the migration can vary significantly between years. Data from Fiskevårdsteknik AB.

The spawning migration of sea lampreys is an almost strictly nocturnal phenomenon, where daylight hours are spent sheltered under large stones, in deep recesses, under riverbanks etc. Dense underwater vegetation and collections of woody debris also serve as important hiding places (Andrade *et al.*, 2007). In studies with traps in North America, 98 to 99% of the catches were made at night (Hardisty, 2006). During the spawning migration, lampreys stop feeding, and their tissues gradually disintegrate. They then live off their fat reserves until spawning.

Migration capability

Compared to more highly developed fish, lampreys are weak swimmers with poor endurance. The closed gill system means that they cannot allow oxygen-rich water to passively flow over their gills. Instead, they rely on pumping water in and out of the gill sacs, a process hindered by active swimming as the pumping muscles are usually contracted, and the mouth is tightly closed. The anguilliform swimming mode, with the head constantly moving from side to side, is much more energy-intensive compared to that of fish. It is estimated that the energy cost for a sea lamprey during upstream migration is about five times higher than that of an eel (Hardisty, 2006).

In the absence of challenging migration barriers, sea lampreys swim at a calm and energy efficient pace, primarily utilizing red muscle groups. Stronger currents are overcome through short periods of explosive swimming followed by resting periods where they anchor to the bottom whilst gathering new strength. During the brief but intensive attempts to bypass obstacles, white muscle fibres are primarily used, making the behaviour highly energy demanding. Therefore, difficult-to-pass obstacles significantly deplete the energy reserves of sea lampreys and may negatively impact spawning success (Quintella *et al.*, 2004). The substantial energy expenditure and the bodily changes associated with spawning, where the fish's muscle mass is literally broken down, result in a gradual deterioration of swimming ability as the spawning period approaches (Hardisty, 2006). Lampreys that have significant delays in migration are thus at risk of being in poor condition for successful spawning, or in the worst case, may not reach the spawning grounds.

Sea lampreys usually handle migration barriers differently than salmonid fishes. Instead of jumping over or through falling water masses, they primarily seek refuge in the pocket under the falling water to find a way around the obstacle (Hardisty, 2006). This behaviour works best at natural migration barriers with varied bottom structures. However, if the barriers are entirely vertical with a homogeneous structure, even low falls can constitute absolute migration barriers. In a tributary to Lake Huron, sea lampreys pass two natural waterfalls of 1.4 and 1.5 m. However, the artificial migration barriers used in North America to prevent sea lamprey spawning migration are normally only 40 to 60 cm with an overhang of 15 to 30 cm (Hardisty, 2006; Reinhardt *et al.*, 2009). As the migratory ability of lampreys drastically decreases with the degree of starvation and sexual maturity, even small obstacles far upstream in water systems can serve as absolute migration barriers.

Marking experiments on sea lampreys have shown migration speeds averaging 1.7 kilometres per day for a total distance of 60 km in streams where migration barriers do not exist (Hardisty, 2006).

Habitat

The life cycle of the sea lamprey means that the species is dependent on vastly different environments throughout its life. Coastal river systems, including both major rivers and smaller tributaries, are utilized for reproduction. The habitat choice during the marine phase spans from shallow estuarine environments to deep waters in the open sea. From a national conservation perspective, the presence of spawning areas with proximity to suitable larval habitats holds the greatest significance, and these two environments are therefore described in more detail below.

Breeding areas

The basic requirements for successful lamprey spawning include rivers and streams with a varied river bed of sand, gravel, and stones in various size fractions. The spawning behaviour of the lamprey species found in Sweden has significant similarities, but differs in terms of the coarseness of the substrate and the stream velocity over the spawning grounds.

The spawning sea lamprey typically chooses environments with relatively fast flowing water and the presence of coarse bottom substrate (Figure 22). Spawning grounds often coincide with those of salmon (Igoe *et al.*, 2004; Söderman & Ljunggren, 2009; Åberg & Thorsson, 2010). The substrate of sea lamprey spawning grounds in watercourses in Halland was dominated by stones 5 to 15 centimetres in diameter, often with a mixture of sand and smaller boulders (Söderman & Ljunggren, 2009; Åberg & Thorsson, 2010). Studies of the stream velocity over sea lamprey spawning grounds have shown speeds of between 0.3 and 2 m/s (Maitland, 2003).

Figure 22. A popular spawning ground in river Rolfsån, Halland. A fast-flowing stream with suitable breeding substrate just upstream from a large hollow where the larvae can live buried for 5–7 years before metamorphosing and swimming out to the sea. Photo: Nils Ljunggren.

Watercourses with a sufficiently high stream velocity and erosive force, are required to ensure suitable environments for sea lamprey spawning. Stream velocity may depend on the gradient, but is also influenced by the width of the watercourse. Even watercourses with relatively low gradients can have suitable breeding areas for sea lamprey in narrow sections, where the water flow is significantly compressed. The presence of larger backwaters with soft sediments for growing sea lamprey larvae most likely plays a crucial role in determining how well a watercourse is suited for sea lamprey.

Nursery areas for larvae

The characteristics of an optimal habitat for lamprey larvae can fundamentally be summarised by three important factors (Applegate, 1950; Hardisty, 2006; Söderman & Ljunggren, 2009; Taverny, 2012):

- The bottom should be soft enough for lamprey larvae to burrow.
- The sediment structure should be porous enough to allow the passage of water and food particles.
- The sediment surface should be stable enough to allow for growth (e.g., diatoms) and sedimentation (fine detritus) of food particles.

Environments with suitable nursery areas in form of sediment banks, occurs where water slows down or is impeded, in backwaters, behind rocks, fallen trees, or similar structures, among plant roots and in porous shoreline areas (Malmqvist, 1982; Hardisty, 2006) (see Figure 24). These conditions and structures are often found in naturally meandering watercourses. There is a clear positive correlation between the amount of coarse woody debris (logs >10 cm in diameter, and longer than 50 cm/m^2) and the occurrence of lamprey larvae in watercourses (Figure 23), and areas with many larvae often have a high presence of detritus (Söderman & Ljunggren, 2009).

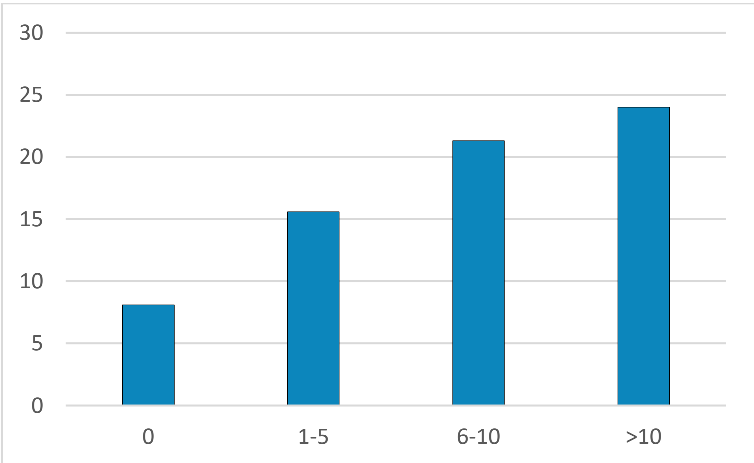

Figure 23. Percentage (%) of electrofishing occasions with the capture of lamprey(y-axis) in relation to the quantity of coarse woody debris (number of logs at least 10 cm in diameter and at least 50 cm long/100 m^2) at the electrofishing site (x-axis). Results from sites located below 300 m above sea level, fished with direct current (DC) electrofishing units during the period 1990–2018. Data from SERS (Swedish Electrofishing Register) 2019-05-24.

Locations with high larval densities are often well separated from the main current of the watercourse, or even located in backwaters with a reverse current direction (Figure 25, 26; Taverny, 2012). The average stream velocity at sites with high larval densities rarely exceeds 0.03 m/s (Maitland, 2003). Lamprey larvae avoid light (Hardisty, 2006), and any form of shade and protection can therefore have a positive effect on the selection of a nursery area.

Figure 24. Sediment banks that provide suitable nursery habitats for lamprey larvae are often formed in the inner curve of meander bends or, as in the photograph, behind a fallen tree. Photo: Micael Söderman

Figure 25. The larger hollows and sediment banks of watercourses are very important nursery environments for lamprey larvae. The photograph shows a sediment bank in river Stensån in Halland. Photo: Micael Söderman.

Figure 26. A typical environment for lamprey larvae: an area dominated by fine sediments close to the shoreline. Photo: Micael Söderman

There are no known differences in habitat and food selection among larvae of sea, river, and brook lamprey, and in waters where the three species coexist, the larvae are found side by side. In mixed populations, larvae from sea lamprey typically constitute only a small proportion (1–6%) of the total larval population (Holčík, 1986; APEM, 2003; O'Connor, 2004; Gardiner *et al.*, 1995; Hardisty, 2006). Targeted electrofishing in Halland streams in 2008 showed that the proportion of sea lamprey larvae varied between 1 and 47%, with a median value of 4.3% (Söderman & Ljunggren, 2009). Under favourable conditions, lamprey larvae can occur in densities exceeding 100 individuals per square meter (Gardiner *et al.*, 1995).

Most studies conducted to examine the quantity of lamprey larvae have been carried out using electrofishing, and are thus limited to relatively shallow waters. In a study where larvae were collected from sediment randomly sampled across all depths, it was found that sea lamprey larvae occurred at depths greater than 2 meters (Taverny *et al.*, 2012). Thus, surveys using electrofishing do not provide a complete picture of the occurrence of sea lamprey larvae in a watercourse.

Lamprey larvae can drift long distances (>1500 m) downstream to reach suitable growing areas (Derosier *et al.*, 2007). However, a strong correlation has been demonstrated between larval density and distance to spawning grounds (Almeida & Quintella, 2002). High larval densities appear to increase the mobility of larvae and their spread to new areas with less competition.

Important inter-species relationships

Large lamprey species, such as the sea lamprey, have a significant impact on the riverbed within their spawning grounds (Sousa *et al.*, 2012; Hogg *et al.*, 2014). By moving away all larger stones from the spawning nest, depressions are created in the riverbed with sand and gravel, while larger fractions are piled up at the side of the depression and flushed clean of finer particles.

Free-living and web spinning caddisflies and stoneflies were found in an American study to occur in up to ten times higher densities in stone piles created by sea lamprey compared to the actual redds or unaffected reference areas (Hogg *et al.*, 2014). It seems that the lampreys' sorting of the substrate increases the number of habitats for benthic fauna, and simultaneously creates a more varied aquatic habitat with hiding places for small fish. The piles of clean, coarser gravel and stone materials deposited adjacent to the redds provide the riverbed with spawning substrate for salmon and sea trout the following autumn (Igoe *et al.*, 2004; Ljunggren, 2007; Söderman & Ljunggren, 2009).

Impact on parasitised animals

The ability of a host animal to cope with a sea lamprey attack depends on the size relationship between the parasite and the host. A significant percentage of blood loss results in rapid blood dilution, where lost blood is replaced with more blood plasma at a higher rate than new blood cells can be formed. Healed scars from sea lamprey attacks on large fish and marine mammals indicate that attacks from sea lampreys are often survived. However, for smaller fish or repeated attacks with prolonged blood loss, the outcome can, in many cases, be fatal (Hardisty, 2006).

Suitability as a signal or indicator species

The sea lamprey's life cycle, with requirements for various well-functioning habitats and processes, makes it a good environmental indicator. In larger populations, it often signifies a natural river environment with good connectivity and high structural complexity. The species needs both running water for its spawning and stable sediment banks in slow flowing water for the larvae's growth. Additionally, it requires a healthy sea with large fish and marine mammals that it can parasitise.

The fact that the species is relatively easy to survey during its freshwater phase makes the sea lamprey a highly suitable umbrella species for larger coastal watercourses.

Distribution and threat situation

History and trends

In Sweden, the sea lamprey has not been used as human food nor is it important for sports fishing, which limits the available information regarding historical distribution and occurrence. However, compilations of historical records made during the 2008 inventory in Halland, which included interviews with present and former County administrative board officers and many local residents, as well as studies from river Örekilsälven in Västra Götaland, suggest that the species was much more common in the past (Söderman & Ljunggren, 2009, Åberg & Thorsson, 2010).

Causes of decline

Changes in freshwater habitats

Hydroelectric power

The activity that probably has had the most negative effect on the Swedish sea lamprey population is the construction of hydroelectric power plants. The dams have cut off the species from large areas with suitable spawning and nursing habitats. Therefore, the construction of new hydroelectric plants in watercourses where the species is present must be considered a significant threat, even though new hydroelectric plants are relatively uncommon today.

The sea lamprey's lack of true homing behaviour suggests that the exploitation of other European watercourses could also negatively impact the number of spawning sea lampreys in Swedish watercourses. This should particularly apply to geographically neighbouring watercourses with outlets in the North Sea, Skagerrak, and Kattegat.

Alongside the numerous barriers that hydroelectric power has created, rapidly fluctuating water levels and unnatural water regulation pose a risk of draining spawning and nursing areas, or even washing away sediment. In such a case, single events can affect several generations of lamprey larvae. The establishment of power plants and dams also causes direct physical changes in the aquatic environment by impounding upstream sections of the river, while downstream sections are cleared and channelised to reduce flow losses.

Fishways have been constructed at many hydroelectric plants and dams. However, the sea lamprey is considerably less adept at navigating obstacles than, for example, salmon and sea trout. Therefore, traditional fish ladders with vertical weirs, as built at many artificial obstacles, function poorly or not at all (Figure 27). It is essential that future fishways are designed to allow sea lampreys and other species lacking the ability to pass vertical barriers to pass both upstream and downstream.

Figure 27. Classic pool-and-weir fishway with vertical drops between resting pools are impassable for sea lampreys. It is important that more naturally designed fishways are implemented in future water conservation efforts. The photograph shows a chamber lock in river Fylleån, Halland, where there are large upstream areas suitable for sea lampreys. Photo: Nils Ljunggren.

Removal and destruction of larval nursery areas
Channelisation and clearance of watercourses poses a significant threat to the nursery areas of lamprey larvae. Several watercourses where the species occurs are wholly or partially subject to land drainage activities and, consequently, are at risk of being cleared.

Stone paving of the river margins can occur for various reasons. In built-up areas, it often happens for aesthetic purposes. Another common reason is to prevent erosion by lining banks with stone. Stone-paved and walled shores commonly prevent fine sediment from accumulating.

Deep pools and backwaters have traditionally been viewed negatively in fisheries management because these environments attract pike and other species that prey on salmonid fish. Therefore, such features have sometimes been altered or removed.

Changes in the marine environment

Availability of suitable hosts

Since the 1940s, the numbers of large fish have decreased significantly in the North Sea, Skagerrak and Kattegat. Fully-grown individuals of species such as cod, whiting, and haddock have become increasingly rare during the last few decades (Svedäng *et al*., 2004). The lack of a sufficient number of large host fish most likely has a negative impact on the survival and growth of the sea lamprey in the marine environment.

Current distribution

The sea lamprey is found on both sides of the Atlantic Ocean. The species occurs in rivers from Labrador to Florida along the Atlantic coast of North America. In the eastern Atlantic, the species is found from central Norway southwards along the coasts of Europe, including the British Isles, in the western Mediterranean, and eastwards to the Adriatic Sea (Holčik, 1986; Figure 28). Single specimens have been found, probably during feeding migrations, up to Varangerfjord in northern Norway, in Iceland, and along the coast of Greenland.

Figure 28. Distribution of sea lamprey in Europe. Schematised according to Holčik (1986) and GBIF.org.

In Sweden, reproducing sea lamprey occurs along the coast from northwest Skåne to the Norwegian border, with a historical stronghold in Halland and Västra Götaland Counties. The species occurs rarely in the southern Baltic Sea, where adult fish have been observed in e.g. river Skräbeån and river Mörrumsån. Occasional records have been made in river Dalälven and in river Rickleån in Västerbotten in northernmost Sweden.

During the 2008 survey in Halland, reproduction of sea lamprey was noted in all salmon-bearing watercourses except rivers Törlan, Tvååkersån, Himleån, and Löftaån (Söderman & Ljunggren, 2009). In later surveys, the species has also been found in river Löftaån (Ingvarsson, 2016). The largest spawning population occurs in river Ätran. However significant upstream migration probably occurs in river Viskan with its tributaries, where the species has been found in the tributary Surtan.

The occurrence in Västra Götaland is not fully investigated. Observations exist from river Göta älv, including tributaries such as Säveån, Grönån, and Lärjeån. Sea lamprey is also found in river Örekilsälven, and in river Enningdalsälven, where spawning lampreys have been encountered on the Norwegian side of the river.

The species is very rare in Skåne. Regular upstream migration occurs only in river Rönne å, mainly in the tributary Rössjöholmsån, but the number of spawning fish appears to be very small. Occasional spawning has been observed in river Råån river. A few individuals have been observed in rivers Helge å and Skräbeån.

A summary of known Swedish records is presented in Appendix 2.

Figure 29. Rivers with records of spawning migratory sea lamprey in southern Sweden. Black circles indicate main watercourses with regular occurrences, white circles represent water courses with occasional records after year 2000. Isolated records have previously been made in river Dalälven and river Rickleån in Västerbotten, northernmost Sweden.

Current population facts

During the 2008 survey of sea lamprey in Halland, spawning sea lamprey was recorded from 9 main watercourses (Figure 29, Appendix 2). Except for river Suseån, larvae were found in all these rivers during subsequent electrofishing. Based on the number of observed individuals, the number of observed redds, and their size, it was estimated that between 500 and 1000 sea lampreys were spawning in Halland in 2008 (Söderman & Ljunggren, 2009).

In surveys conducted in Halland in 2015 and 2016, the species was found in 20 rivers (i.e.7 main watercourses), with a total of about 200 individuals observed. In 2017, the species was found in 12 rivers (i.e.7 main watercourses). In 2018, the species was found in 9 rivers, with a total of 50 individuals. During the 2019 surveys, the species was only found in 2 rivers, with a total of 26 individuals observed.

In connection with a survey in Västra Götaland in the summer of 2019, sea lamprey was observed in 2 watercourses, with a total of 10 individuals. A few redds were observed in an additional watercourse.

Surveys conducted in Skåne in 2017 and 2018 found neither redds nor sea lamprey larvae. Three dead sea lampreys were found in the lower part of river Rössjöholmsån in the summer of 2017. The population in Skåne is doubtless very small.

An overall assessment is that the Swedish spawning population amounted to fewer than 100 individuals in 2018 and 2019 (P. Ingvarsson, pers. comm.).

The surveys conducted during the period 2015-2019 are not quite as extensive as in 2008, and the number of spawning individuals in recent years may be somewhat underestimated. However, there is no doubt that the species has gradually disappeared from several previously known spawning waters during the 2010s.

Updated population facts 2020-2023[2]:

Yearly surveys have been performed in Halland and Västra Götaland covering all watercourses where spawning can be expected (see Table 1).

[2] updated and added in the English language version.

Table 1 Updated population facts 2019-2023 (*including fish counter data from Herting, river Ätran, Halland).

	Sea lampreys observed 2019-2023 (yearly counts)	Redds observed 2019-2023 (yearly counts)	Main watercourses with sea lampreys (annual number)
Halland	21/69/134/53/28*	19/69/73/23/34	2/5/5/5/3
Västra Götaland	10/15/22/23/13	22/91/59/41/47	2/3/3/3/2

As for Skåne surveys for redds in the rivers Rössjöholmsån (2019, 2020, 2021), Bäljane å, Pinnån and Rönne å (all 2021), all part of the same main watercourse, did not result in any redds found. However, one adult sea lamprey was caught in river Rönne å during 2022 and two adults during 2023 when electrofishing from boat.

Current threat situation

The sea lamprey was classified as Near Threatened (NT) on the Swedish red list in 2015 (Swedish Species Information Centre, 2015). The assessment was based, in part, on the assumption that no spawning population exceeds 300 individuals, and the estimated number of reproductive individuals in the country was assessed to be 1800 (1200–2500). At that time, there was uncertainty about the population trend, but it was considered likely that the species was declining due to continued significant human impact upon its habitats. The lack of large host fish in the sea was also expected to have a negative impact on the species.

In the 2020 Swedish red list, the species is classified as Endangered (EN) due to a drastic decrease in numbers.

In HELCOM's red list (2013), the sea lamprey is listed as Vulnerable (VU). On the IUCN Global and European red lists (IUCN Red List of Threatened Animals), the sea lamprey is classified as Least Concern (LC) (Nature Serve 2013). The justification for this assessment includes its extensive distribution area, the large number of populations and individuals, and the absence of significant threats.

European red list assessments range from Regionally Extinct (RE) in the Czech Republic to Near Threatened (NT) in Norway and France. In Italy, the species is classified as Critically Endangered (CR), and in Poland, it is classified as Endangered (EN). Croatia lists the species as Data Deficient (DD) (nationalredlist.org).

Probable effects of various expected climate changes

Knowledge about how the sea lamprey might be affected by climate change is very limited. Cline *et al*. (2014) suggest that sea lampreys in the Great Lakes in the USA could be positively influenced by increased temperature because, with higher water temperatures, they can consume more food and thus experience increased growth. However, it is unlikely that the North Sea will become significantly warmer in the foreseeable future. Therefore, the sea lamprey's nutritional status is unlikely to be affected.

Nevertheless, climate change may lead to altered water flow in rivers throughout the year, which could have negative consequences for both adult individuals and larvae. Increased risk for flooding in the wake of climate change could negatively impact larvae. Some rivers may receive new embankments and be stone lined, thereby degrading or eliminating the sea lamprey habitats. Ocean warming also gives rise to large scale changes in fish fauna, where cold water species are replaced by those with higher temperature preferences. It is unknown what effects this may have on the sea lamprey.

Legal protection

The sea lamprey has the following status in national legislation, EU directives, EU regulations, and international agreements ratified by Sweden. EU directives are incorporated into Swedish legislation through laws and regulations. EU regulations are directly applicable as law. The text below only addresses legislation, etc., where the species has been specifically identified in annexes to directives and regulations. General legislation that may affect a species, or the habitat type or area where the species occurs, is not included in this overview.

National legislation

The sea lamprey is designated with restrictions in the regulations of the Swedish Agency for Marine and Water Management (FIFS 2004:36) regarding fishing in Skagerrak, Kattegat, and the Baltic Sea, as well as in the regulations for freshwater areas (FIFS 2004:37). It is stipulated that intentionally catching or killing sea lampreys is prohibited. Any sea lamprey caught unintentionally must be immediately released where it was caught. This applies even to dead individuals. Thus, all capture of sea lampreys is prohibited, even for scientific purposes. Any handling of the species requires a permit.

EU legislation

The sea lamprey is listed in Annex II (animal and plant species of community interest whose conservation requires the designation of special areas of conservation) of the Habitats Directive, on the conservation of natural habitats and of wild fauna and flora (Council Directive 92/43/EEC, most recently amended by Council Directive 2013/17/EC). In connection with EU accession, Sweden negotiated an exemption from the requirement to designate specific protected areas for all lampreys. However, the requirement to achieve and maintain a favourable conservation status for all three lamprey species still applies. Population size, distribution, prospects, and threats is reported in the same manner as for other species in Annex II.

International conventions and action plans

The sea lamprey is listed in the Bern Convention, Appendix III protected species (Convention on the Conservation of European Wildlife and Natural Habitats, Bern, September 19, 1979 (SÖ 1983:30). This commitment implies that the habitat where the species is found must not be exploited unless the exploitation does not endanger the population. The national protection through regulations by the Swedish Agency for Marine and Water Management aligns with the commitments Sweden has under the Bern Convention.

The Convention for the Protection of the Marine Environment of the North-East Atlantic, OSPAR, lists the sea lamprey as a threatened species. Signatory parties commit to protecting the species and its habitats. The measures expected, from member states where the species is present, are outlined in a recommendation from 2015 (OSPAR 15/20/1, Annex 7). Emphasis is placed on the need to secure and restore sea lamprey habitats with access to free migration routes, good water quality, and undisturbed habitats. OSPAR emphasizes the need for involvement from relevant sectors such as agriculture, industry, and fisheries. Countries are obligated to report progress every six years, starting from 2019, following the initial report in 2016.

According to the Ramsar Convention (the Convention on Wetlands), particularly valuable wetland areas may be designated as Ramsar sites based on nine criteria. In the Ramsar site river Fylleån, the sea lamprey is included as one of the species that fulfils three of the criteria. In the Ramsar site river Helge å, the sea lamprey is mentioned in the area description as an important species.

Other facts

Experiences from previous measures that may affect conservation work

In recent years, two major restoration projects have been carried out in the watercourses of Halland. The restoration of free migratory routes in the Rolfsån water system and the removal of the holding dam at the Herting power plant in river Ätran. Together with the bypass around the Hedefors power plant in river Säveån, a tributary to river Göta älv, these measures are the first where free migratory routes, allowing for all fish species to pass, have been restored in watercourses where the sea lamprey occurs. In both river Rolfsån (Ålgårda power plant) and river Ätran, monitoring with camera surveillance shows that sea lampreys have passed the previously impenetrable migration barriers in the first summer.

Capture and upstream transport have been carried out manually in connection with the former pool-and-weir fishway at Herting in river Ätran. Migration data from 2014 and 2015 indicate a more concentrated migration period compared to the years before the new fishway was in place, when spawning individuals tried for several weeks to find a way for upstream migration (Calles *et al.*, 2015) (Figures 20 & 21). The cold early summer of 2015 saw a highly concentrated migration with practically all ascent occurring over three days.

After extensive restoration and long-term liming efforts, river Himleån now has free migration routes and relatively good water quality. Salmon has been spawning successfully in the main river since the early 1990s (L-G. Pärlklint, pers. comm.). In addition, both sea trout and salmon have been able to recolonise parts of the catchment area where they previously had been wiped out. Even though the river and several of its tributaries should be very well suited for all lamprey species, the presence of lampreys could not be proven either during the extensive targeted inventory in 2008 or during the follow-up inventories in 2015-2019 (P. Ingvarsson 2019, pers. comm.). Nor have lampreys been observed in any of the many electrofishing surveys carried out in the river over the years. It is likely that the lack of lamprey larvae means that the watercourse has low attraction for mature lampreys, and that spontaneous recolonisation has therefore failed. The phenomenon is known from the Great Lakes in North America, where chemical culling of larvae is used as a method of eradicating sea lampreys from a watershed by reducing the attractiveness to spawning adults (McDonald & Kolar, 2006).

Downstream passage at power plants

Moser *et al.* (2014) summarise the state of knowledge on how juvenile lampreys are affected by power plant passages during downstream migration. The authors note that the morphology and anatomy of lampreys, including the absence of a swim bladder, scales and hard bone structures compared to bony fish, make them significantly more resistant to the stress of a turbine passage. In laboratory experiments simulating the severe pressure changes, high water pressure and risk of direct physical damage of the kind that occurs in a water turbine, juvenile Pacific lamprey *Entosphenus tridentata* showed high resilience and low mortality (Colotello *et al.*, 2012 in Moser *et al.*, 2014).

Lampreys, with their limited swimming ability and elongated body, are at high risk of being drawn into power turbines. Unfortunately, many structures designed to divert and protect salmonids at water intakes are not suited to lamprey and can result in greater harm than unscreened intakes. In the United States, it has been noted that steeply slanting grids and finely meshed nets (2-5 mm) often are ineffective for lampreys, as there is a risk that they get impinged with no possibility of escape (Moser *et al.*, 2014). However, this risk is very small in Sweden where turbine intake diversion screens generally have a gap width of 15 mm or larger. Solutions can be found to minimise mortality for both lamprey and bonefish, by considering differences in circadian rhythm, migratory season and behaviour. Important differences from salmon and trout smolts are that lampreys often swim in the thalweg, close to the riverbed, are almost strictly nocturnal, avoid white light and, not least, have their downstream migration concentrated to the autumn.

A general conclusion is that lampreys may require special consideration to secure their downstream migration.

Fishery management for salmon and sea trout

In many of the watercourses where sea lamprey spawn, extensive measures have been implemented to favour stocks of salmon and sea trout. Generally, these measures have resulted in major nature conservation benefits. Cleared stretches of watercourses have been restored to more varied habitats of value to many fish species, benthic fauna and large freshwater mussels. Since many former stretches of running water have disappeared, or are inaccessible after dam construction and related flooding, there is both a major economic (smolt production) and nature conservation (running water habitats) interest in re-creating and improving the environment in watercourses. When rivers are rehabilitated in order to create habitat for salmon and sea trout, this often have led to the disappearance of backwaters and nursery areas for larval lampreys. For all lamprey species, it is necessary to aim at more varied watercourses to ensure successful reproduction and completion of the life cycle.

Experiences from contending with sea lamprey in North America

Like many other marine and anadromous fish species, sea lamprey has developed entirely freshwater ("land locked") populations, which spend their parasitic phase in larger lakes. Sea lampreys occur naturally in several lakes along the east coast of North America, including Lake Ontario. Upstream of Lake Ontario, further migration was prevented by the Niagara Falls. With the completion of the fourth Welland Canal in the 1930s, sea lampreys were able to migrate upstream, and by 1946 the entire North American Great Lakes system and many tributaries had been colonised (Brant, 2019). This new species to the lake ecosystem quickly had a major impact on the fish fauna, and it is still seen as one of the worst examples of the impact of invasive alien species globally. In Lake Huron, the annual catch of various trout and char species before 1940 was between 1800 and 2700 tonnes. By 1954 the catch had fallen to 76 tonnes, and in 1959 the fishery collapsed completely. The trend was similar in the other Great Lakes (Hardisty, 2006).

Much of the sea lamprey research carried out over the years has been aimed at developing methods to control the species in the Great Lakes. Important knowledge that is also useful for conservation work in areas where the species occurs naturally is knowledge of the species' ability to cross migration barriers, the lack of homing behaviour and the larvae's production of substances that attract spawning adults.

Vision and Objectives

Vision

The sea lamprey has a favourable conservation status. Consequently, the species occurs in strong populations in watercourses throughout its original Swedish range.

The value of the sea lamprey as an umbrella species is utilised in nature conservation.

Long-term objectives (2040)

- Stable and viable populations exist in all major salmon-bearing rivers, including at least one tributary, from Västra Götaland to Skåne. Annual spawning should take place in all suitable watercourses within the range.
- Sea lamprey larvae shall be present in suitable nursery areas downstream of natural migration barriers for the species.
- Measures shall be taken in all rivers where sea lampreys are present to ensure that sea lamprey and other fish species that lack the ability to pass vertical barriers, have access to at least one area of spawning habitat, together with larval nursing areas, in the main channel. In larger rivers, suitable habitats should also be available in at least one tributary.
- In watercourses with known occurrences of sea lamprey, functional fish passage solutions have been implemented to ensure that sea lamprey, and other fish species lacking the ability to pass vertical barriers, can pass safely upstream.
- Measures have been implemented to ensure safe downstream passage for migrating juvenile sea lamprey past hydroelectric power plants.
- Enough water should be released into fish passages when sea lamprey migrate. If sea lamprey cannot pass a hydroelectric power plant and choose to spawn downstream, enough water should be present where they spawn and during the subsequent three weeks needed for the eggs to hatch and the larvae to disperse downstream.
- The host fish in the sea should have a size and age distribution that maintains ecosystem functions with abundant large fish.
- Habitat management has been conducted to restore and create nursery areas for larvae, where possible and justifiable.
- Stretches of watercourse that are important for sea lamprey larvae are allowed to develop naturally and have been protected from exploitation. If exploitation cannot be avoided, compensation measures are required to restore the lost area of suitable nursery areas.

- Affected county administrative boards, in dialogue with soil drainage communities (Swe: dikningsföretag), have created plans to limit negative impacts on the sea lamprey.
- Protected areas have been established in watercourses with significant occurrence of sea lamprey.

Short-term objectives (2024)

- There shall be no reduction in available spawning and nursery areas.
- The status and distribution of the sea lamprey in Sweden is known. Identification of occurrence and status has been completed in all salmon-bearing watercourses in Västra Götaland, Halland, Skåne, and Blekinge.
- The possibilities for sea lamprey to safely pass existing fish passage solutions, both upstream and downstream, in salmon-bearing watercourses within its range has been investigated.
- Soil drainage communities active in watercourses with sea lamprey, have been informed of the importance of preserving nursery areas for larvae.
- Relevant authorities are working actively to establish the sea lamprey as an umbrella species for conservation work in major rivers in Västra Götaland, Halland, and Skåne.
- A national monitoring program has been established. Monitoring takes place in selected watercourses at intervals of maximum 6 years in accordance with the reporting requirements of Article 17, the Habitats Directive.
- Relevant authorities have set prioritisation plans for actions to increase the area of spawning and nursery grounds.
- A review of the national incorporation of international commitments for the species has been conducted, and if necessary commitments have been clarified.
- Relevant authorities take the environmental requirements of the sea lamprey into account, when hydroelectric power plants are re-evaluated to align to contemporary environmental requirements.
- The regulatory guidance developed within the framework of a national plan for the reassessment of hydroelectric power considers the sea lamprey's environmental requirements regarding upstream and downstream passage, as well as other aspects such as sedimentation and erosion.

Deficiency analysis

Measures aimed at addressing migration barriers generally entail water operations requiring an adjudication from the Land and Environment Court. It may also require an exemption/permit from shoreline protection according to the Environmental Code. In most cases, the suggested measures also imply an intrusion into ongoing economic activities, as they may affect both commercial and private interests. The fact that the measures themselves are expensive to implement, means that both planning and implementation measures are long-term processes that require good planning, well defined legislation, established judicial practice, and sufficient financial resources.

Habitat restoration measures in southern Sweden's watercourses have until present days primarily focused on strengthening salmon and sea trout populations. Slow flowing stretches with silty and sandy riverbeds have been overlooked, or even seen as lacking importance for the biological values of the watercourses. Such areas have even sometimes been actively “restored” in order to gain stream habitats, and to reduce the potential negative impact of pike and other predatory fish.

Actions and Recommendations

Description of actions

This section contains a general description of the measures proposed to be implemented during the validity period of the action plan. A table with more information about the planned measures appears in Appendix 1.

Targeted surveys of sea lamprey have not yet been conducted in all counties. Such surveys must be completed to provide a basis for further prioritisation of measures within the action plan.

Experiences from Halland show that watercourses with a permanent presence of salmon also have the prerequisites to accommodate spawning sea lampreys. Therefore, in addition to watercourses with a known presence of sea lamprey, salmon-bearing watercourses in Skåne and Västra Götaland are prioritised for measures. The conclusions of the action plan, as well as general proposals for measures, can thus be directly applied in conservation work also in these watercourses.

A more holistic approach is required when restoring watercourses, for future water management measures to better benefit lampreys and other species requiring a complex and varied aquatic environment. There is an ongoing shift in attitudes to migration barriers, with the removal of the barrier or the creation of more natural bypasses now seen as alternatives to more technical solutions. It is important that this practice is maintained, not least in the future where a change in water legislation leads to mandatory measures with an additional number of private actors and commercial operators taking the initiative. The county administrative boards have an important role in ensuring that proposed measures are adapted to the natural conditions of the watercourses and to all existing species.

An important measure is to assess passability for sea lamprey and other species less prone to pass vertical obstacles at existing migration barriers.

It is vital that appropriate authorities have an ongoing national and international information exchange in order to be able to develop knowledge-based management, for example regarding suitable measures at migration barriers.

Information and advice

When writing new, or updating existing, handbooks on watercourse restoration, consideration should be given to how to handle both existing nursery areas for sea lamprey and the creation of new ones. The value of the sea lamprey as an indicator of a functioning running water ecosystem should be emphasised. The important role of the species in watercourses should be evident, not least the restructuring and diversification of the riverbed at spawning.

It is suggested that an information brochure be produced to increase knowledge about the sea lamprey and its environmental requirements. The brochure should be concise and promote interest, focusing on the environmental requirements of lampreys in relation to free migration routes and healthy watercourses and seas. The target audience includes landowners, stakeholders, the general public, local fisheries management organisations (Swe: fiskevårdsområden), community associations, and fishing rights owners who own and manage fishing waters.

There is still a misconception that sea lamprey pose a threat to salmon and sea trout in rivers. Information signs are therefore suggested for strategic locations, stating that the species is red-listed and protected, and showing the life cycle of the species, emphasising the ending of food intake during the spawning migration.

Education

Currently, only a few individuals in Sweden have experience of working with measures for sea lamprey and possess the knowledge of the environmental requirements and ecology of this organism group necessary to conduct targeted surveys.

Relevant authorities should organise one or more training sessions early in the program period for their own staff, local fisheries management organisations, fishing rights owners, external consultants, community associations, and others who will be involved in the proposed measures in the action program. Examples of topics that should be included in the training are:

- How to identify various species of lamprey, both in their adult and larval stages.
- Differences in the lamprey species' habitats, life histories, and the traces they leave behind.
- General environmental requirements for lampreys.
- What defines a suitable environment for sea lamprey larvae, and how to identify it.
- Sea lamprey behaviour during spawning migration.
- Spawning behaviour and surveying spawning sea lamprey. When and where to search and what to look for.
- Electrofishing for sea lamprey larvae.

New knowledge

There are several uncertainties that need clarification in order to move towards a more knowledge-based management of sea lamprey in Sweden. In addition to research initiated by Swedish universities and colleges, collaboration should be established with ongoing research projects in e.g. Portugal, France, Belgium, and Ireland. Much experience can also be drawn from work in North America's Great Lakes.

Key questions include:

- Increased knowledge about the downstream migration of metamorphosed juveniles, especially how sea lamprey cope with passing through hydroelectric power turbines and intake screens when attempting to reach the sea.
- How synchronised is downstream migration to the sea?
- To what extent is sea lamprey philopatric? How much exchange occurs among Swedish watercourses, and between those in other countries?
- Comprehensive studies of larval occurrence in different environments and water depths. How accurately does electrofishing provide a picture of the actual distribution and species composition?
- How far into the estuary areas of watercourses are larvae present in the sediment, and how well do they tolerate sea water?
- How does recolonisation occur in areas where sea lamprey regain access to former spawning and nursery areas, e.g. after restoration of free migration routes? Does it happen spontaneously? Or might translocations be necessary?

Surveys

Targeted surveys of sea lamprey should be conducted in order to clearly specify and prioritise the required measures. In the initial stage, surveys can be limited to watercourses that currently have or historically had salmon populations. The suggested approach involves a combination of surveys for spawning sea lamprey and electrofishing for larvae. Existing habitat surveys (Swe: “biotopkarteringar”), known migration barriers, and knowledge of spawning areas for salmonids provide an important knowledge base for these surveys.

More comprehensive knowledge about the status of sea lamprey in Swedish watercourses is only available from Halland, where a survey was conducted in 2008 (Söderman & Ljunggren, 2009). Additional surveys have been carried out in various watercourses from 2015 to 2023 (Ingvarsson, 2016, Ingvarsson in prep.). Consequently, there is a relatively good up-to-date understanding of the species' distribution and status in Halland's watercourses.

The investigations in Halland, combined with surveys of river lamprey in southern Sweden over the last decade, indicate that targeted surveys during the right season and weather conditions are necessary to obtain a thorough understanding of the occurrence and population status of anadromous lamprey species. As an initial step, targeted surveys of both spawning sea lamprey and larvae are therefore suggested in all salmon-bearing coastal watercourses in Västra Götaland and Skåne, as well as Mörrumsån in Blekinge. Supplementary and follow-up surveys are required in Halland.

The following information should be gathered during the surveys:

- Contemporary and historical occurrences of sea lamprey through literature reviews.
- Presence of spawning sea lamprey.
- Presence of sea lamprey larvae.
- Assessment of the ability of lampreys and other species unable to pass existing migration barriers in the surveyed rivers.
- Need for habitat management to create or restore nursery areas for lamprey larvae.

Assessment of population status

The absence of homing behaviour makes it of subordinate importance how many parent fish ascend for spawning in a single year when assessing the status of a watercourse. When evaluating the status of individual watercourses, it is suggested to focus on ensuring that the species has access to as much of the watercourse as possible, and that suitable nursery areas occur downstream potential spawning sites. The presence of larval populations with a healthy age distribution constitutes the best measure of the species' status in the individual watercourse. The high fecundity of the sea lamprey means that these factors are probably more important than the number of parent fish.

Prevention of illegal activities

Measures directly aimed at harming sea lamprey are considered rare, and there is no targeted fishing for sea lamprey in Sweden. However, due to the species' high economic value in parts of Central and Southern Europe, there should be an awareness of the possibility of increased interest for fishing if the migration of spawning fish in Swedish watercourses was to rise significantly.

In some areas along the Swedish west coast there has long been a misunderstanding that sea lamprey during their spawning migration could pose a threat to other fish species, especially salmon. Reports from several watercourses indicate that spawning sea lamprey have been caught by snag fishing or collected and killed (Söderman & Ljunggren, 2009). It is thought that this killing is a decreasing problem, and that it can be mitigated by information being provided at popular salmon fishing locations and near spawning areas for sea lamprey.

Reassessment of existing regulations

Reassessment of environmental permits

The primary obstacle to expanding the distribution and population of sea lamprey in Sweden is the numerous dams that prevent the species from reaching suitable spawning and nursery areas. For most dams in watercourses with sea lamprey, there are at present no opportunities to pass upstream. In cases where fish passage solutions exist, they are rarely adapted for lampreys and other species unable to pass vertical obstacles, or poorly designed and positioned with inadequate functionality (Andersson, 2005; Figure 27).

In most cases, dams and hydroelectric power production cause harm to watercourses by impounding previous running water habitats, submerging sections, and disturbing the naturally fluctuating flow patterns.

Recurring watercourse clearing done by soil drainage communities is generally considered a minor issue in watercourses where sea lamprey is present. However, in places where dredging still occurs, the damage to the larvae and their nursery areas can be extensive. Examples of such watercourses include rivers Viskan, Tvååkersån, Smedjeån, and Stensån.

The county administrative boards, as regulatory authorities, are responsible for ensuring that ongoing water operations comply with current legislation and possess valid permits. In future supervisory work, it is proposed that watercourses holding populations of sea lamprey are prioritised, and that measures for increased environmental consideration be imposed on relevant commercial operations where possible. Regarding inactive soil drainage communities and unauthorised dams, the county administrative boards should initiate supervisory cases to achieve the best possible environmental solutions.

The presence of, and consideration for, sea lamprey should be prioritised within the upcoming task of reassessing existing hydroelectric power to conform to modern environmental standards. Additionally, reviews of management plans and regional collaborative processes should consider the environmental requirements of sea lamprey.

Establishment of no-take zones

Fish stocks in the Kattegat and Skagerrak have undergone significant changes over the past hundred years due to high fishing pressure. Today, most stocks are overfished, and thus occur in small numbers and exhibit a highly unbalanced size distribution, lacking old and large individuals. For sea lamprey, the absence of large host animals poses a risk of impaired growth and survival during the parasitic marine phase.

Sweden is committed to actively promoting fish stocks with a size and age structure that maintains ecosystem functions. This can be achieved through general fishery related measures, the establishment of no-take zones or areas with selective fishing. In addition implementing conservation measures within existing marine protected areas can be considered.

Protected areas

Management in formally protected areas

The action program provides guidance for measures in protected areas. In protected areas, the implemented actions must align with the governing documents for the area, such as purpose, regulations, and management plans, all of which are designed to promote the overall conservation values of the area. A comprehensive assessment should be made of the potential need for revising the management plan, based on the conservation values of the protected area, when sea lamprey occurs in existing protected areas, and the management plan is not compatible with the measures needed to benefit the species and its habitat.

Direct population enhancement measures

Transport of sexually mature sea lamprey past migration barriers

At migration barriers preventing migrating sea lamprey from reaching upstream spawning and nursery areas, it may be justified to discuss temporary solutions while awaiting more permanent measures. For example, relocating fish upstream of partial migration barriers. Moving fish upstream of total migration barriers is not allowed for infection control reasons. Any movement of fish, fish larvae, and fish roe is associated with risks concerning the spread of viruses, bacteria, fungi, or parasites.

Any potential translocation of sea lamprey should be authorised by the county administrative board, according to the Swedish Agency for Marine and Water Management's regulations (HVMFS 2021:7) regarding the stocking of fish and movement of fish in cases other than between fish farms. In the event of fish translocation, it is advisable for the move to occur early during the spawning migration, to ensure individuals have the best possible condition and migratory capability.

Re-introduction of sea lamprey

In cases where free migration pathways have been established in salmon-bearing watercourses, but colonization by sea lamprey has not occurred within five years, it may be justified to attempt to attract sea lamprey using various methods. An example of such a river is Himleån in Halland, where conditions have been assessed favourable since many years.

Initial trials should start by translocating fertilised roe, which is buried near suitable nursery areas. Additionally, efforts to attract migrating sea lamprey using pheromones can be explored. Any translocation of roe should be authorised by the county administrative board, according to the Swedish Agency for Marine and Water Management's regulations (HVMFS, 2021:7) regarding the stocking of fish and movement of fish in cases other than between fish farms.

Restoration and creation of habitats

In addition to the need for free migration routes, emphasis should be placed on preserving and restoring spawning and nursing areas. Such measures include the restoration of cleared river stretches, and the introduction of coarse woody debris and boulders to enhance habitat diversity in the aquatic environment.

Free migration pathways and restoration of watercourses

One of the main reasons for the precarious situation of sea lamprey in Sweden is limited access to suitable spawning and nursery areas due to migration barriers and the impoundment of river stretches.

Measures related to dams are often lengthy and complex processes where different interests conflict with each other. Existing environmental permits, technical constraints, cultural heritage values, and ongoing activities such as energy production are all factors that influence the solution that can ultimately be chosen to minimise damage to the ecology of the watercourse. The discussions below do not consider the actual feasibility of different measures. Instead, the focus is on what needs to be done to achieve the greatest benefit possible in preserving and increasing sea lamprey populations. The measures primarily aim to increase the number of watercourses with viable populations of sea lamprey.

The task of tackling migration barriers has progressed significantly in some watercourses during the last years. The work is primarily carried out by public authorities and non-profit organisations, most often with a focus on improving migration opportunities for salmon and sea trout. In recent years, the focus has broadened. It is also becoming more common for migration barriers to be resolved through private initiatives, or after summons from the county administrative board.

The impact of individual dams is often well researched, and documentation of prioritised measures exist, often in local fisheries management plans and water management action programs.

The overall goal should be to increase the total emigration of sea lamprey juveniles from Swedish watercourses. This means that measures need to be implemented in all watercourses with the potential to hold populations of sea lamprey, and that these watercourses must be protected from negative impacts. Measures should therefore be generally focused on making as large an area of spawning and nursery areas available as possible, and allowing the establishment of larval populations in as many watercourses as possible. The removal of migration barriers is a measure that both creates a free migration route and releases dammed parts of the watercourse.

Secondly, low gradient nature-like bypass solutions should be favoured allowing all species to pass.

Prioritisation of measures at migration barriers

The summary of Swedish occurrences of sea lamprey (Appendix 2) indicates that the species occurs, albeit in low numbers, in most watercourses along the west coast where suitable natural conditions exist.

Preparation of regional prioritisation documents and plans

Regional plans containing site-specific measures and priorities should be developed in cooperation between the counties concerned. The plans should specify the measures needed for the species to achieve and maintain a favourable conservation status. Particular focus should be placed on the need for free migration routes and the release of dammed stretches.

Dams located in lower regions of catchment areas

The first (closest to the sea) dam in a watercourse often has a very significant impact on the ecological functions and natural values of the watercourse. In many cases, the main river channel and upstream tributaries have lost their value for species that cannot pass through pool-and-weir fishways. In addition, dams and power plants in the lower parts of the main channel constitute a bottleneck for fish passing downstream.

Dams constitute migration barriers and lead to the disappearance of rapids and running water habitats close to the coastline. In watercourses with dams located far downstream, the removal of obstacles and recreation of running water environments, should therefore be seen as urgent measures for the conservation of sea lamprey. When removing dams and migration barriers, or other measures that change the hydrological regime, the risks of accidents should always be considered, in particular the risks of flooding, landslides and mudslides.

Dams with high nature values upstream

In watercourses with an otherwise high degree of naturalness, single obstacles can make large spawning and nursery areas inaccessible. When prioritising measures, great importance should be attached to the size of the areas that can be made accessible. To benefit the sea lamprey, measures that provide access to stretches of watercourse with alternating fast and slow flowing sections, should be prioritised.

Habitat management

The sea lamprey's life cycle requires a varied watercourse environment with gravelly and stony spawning environments in the faster flowing sections, together with slow flowing sections and backwaters where sand, silt and organic material are allowed to settle.

The methodology for improving or restoring suitable spawning areas is the same as for favouring salmon and sea trout.

Previous clearing of large boulders and the lack of well-developed riparian zones with old and dying trees, mean that most watercourses lack structures that decrease stream velocity and create conditions suitable for sedimentation. The addition of structures that favour sedimentation should therefore be seen as a prioritised measure in many watercourses. Placing coarse woody debris is the simplest and most effective method of recreating suitable nursery areas. The method is well developed and frequently used in watercourse restoration in North America and elsewhere, but there are still few practical examples from Swedish watercourses.

All work in watercourses should be planned and designed by persons with the necessary ecological expertise, and with consideration for other aspects, such as cultural heritage.

Monitoring

Sweden's commitments to Ospar and the Habitats Directive require reporting every six years on the sea lamprey's population size, trend, range and distribution, habitat availability, and future prospects. The Swedish Species Information Centre (SLU Artdatabanken) has been tasked by the Swedish Agency for Marine and Water Management to develop a suitable monitoring method for the sea lamprey, intending to coordinate this with the monitoring of river lamprey.

Monitoring should be tailored to the sea lamprey's specific ecology and life cycle. The presence of larval populations with a good distribution of different age classes, combined with spawning occurring on suitable bottoms, constitutes the best measure of the species' status in a watercourse. Continuous monitoring of migrating sea lamprey should take place in fishways that are equipped with camera systems.

Follow-up on measures

Structured and targeted follow-up is an important tool to assess whether implemented measures have been effective, and to provide insights into how actions can be further developed for optimal results.

Targeted inventories should be conducted before and after all direct conservation measures carried out within the action program. The presence of larvae of different age classes is the most important indicator for assessment of the outcomes of the measures.

General recommendations

This chapter is intended for all those outside public authorities who come into contact with sea lampreys through their work or leisure activities, whose actions may affect the sea lamprey's situation, and who want guidance on how to act in their favour.

Measures that may harm or benefit the sea lamprey and its habitat

Measures that can harm and benefit the sea lamprey are described earlier in this programme under 'Current threats' and 'Measures and recommendations'.

Financial support for measures

In addition to the targeted funds allocated annually to the county administrative boards for work on the action plans for threatened species, there are a number of opportunities for funding nature conservation projects in the aquatic environment. For many of these funding sources, the conditions for use change regularly, and in many cases co-financing is required. A selection of possible funding sources is listed below:

- EU Rural Development Programmes
- European Maritime and Fisheries Fund
- EU Environment Programme LIFE
- LONA Local Nature Conservation Initiative and LOVA Local Water Conservation Projects
- Fisheries Conservation Fund
- Good Environmental Choice ('Bra miljöval', the Swedish Society for Nature Conservation)

Release of species into the wild for reintroduction, reinforcement or translocation

The motives, conditions and measures for the release must follow the recommendations of the strategy for the release and dispersal of fish (Sparrevik, 2001). The release must be described in detail in a specific release programme. The release programme must follow the guidelines of the Swedish Environmental Protection Agency (Wetterin, 2008) and the guidelines of the International Union for Conservation of Nature (IUCN) (IUCN/SSC, 2013).

In the case of releases, anyone wishing to release threatened plant or animal species protected under Sections 4-9 of the Species Protection Ordinance (2007:845) or protected under Section 5 of the Fisheries Ordinance or Section 3 of the Hunting Act (1987:259), as well as anyone wishing to acquire basic material for breeding and rearing, including storage and transport, must ensure that they obtain the necessary permits. In accordance with Sections 14-15 of the Species Protection Ordinance, the county administrative board may, in individual cases, grant exemptions from the prohibitions in §§ 4-9 that apply to the county or part of the county. The capture and release of mammals and birds requires a permit from the Swedish Environmental Protection Agency. For the storage and transport of live specimens of plant and animal species marked with an N or n in Annex 1 to the Species Protection Ordinance, an application must be made to the Swedish Board of Agriculture for an exemption from the prohibition in Section 23.

In the case of releases, it must be considered that measures that do not require a special licence but that can significantly affect the natural environment must be reported for consultation to the county administrative board in accordance with Chapter 12, Section 6 of the Environmental Code. All types of release and translocation of fish, mussels, or crayfish are subject to authorisation under the Swedish Agency for Marine and Water Management's regulations (HVMFS, 2021:7). The reason is to limit and control the spread of unwanted species, strains and infectious diseases. Permits are applied for through the county administrative board.

Authorities can provide information about current legislation

The owner or custodian of land or water where threatened species and their habitats occur should be aware of how the area is used. Managers who understands the need to maintain or not interfere with the natural values, and show consideration in their use of the area is usually a good guarantee that the species can be retained in the area.

Regardless of the operator's knowledge and interest in conserving natural values, there may be demands on the operator under applicable laws, ordinances and regulations. The authority that oversees the activity or measure in question determines which authority should be contacted in such cases. The county administrative board is the authority that is usually the supervisory authority. For activities covered by the Forestry Act, the supervisory authority is the Swedish Forestry Agency. One can always contact the county administrative board to find out which authority has responsibility.

The supervisory authorities will be able to provide information about the regulations that apply in each case. There may be licensing, notification or consultation requirements. The relevant authority can provide information about necessary contents and time limits, before a notification or application for activities is submitted.

Advice on dealing with knowledge of observations

According to the Freedom of Information and Confidentiality Act (2009:400), Chapter 20, Section 1, information about a species of animal or plant that needs protection, and for which there is an interest in maintaining a viable population, is confidential if it can be assumed that sustainability of the species in the country or part of the country will be adversely affected if the information is disclosed. Spreading of information on the occurrence of threatened species requires discretion, as illegal hunting and collection may pose a threat.

The Swedish Marine and Water Agency's policy is that information should, as far as possible, be spread to landowners and holders of rights to use areas where the species occurs permanently or temporarily, so that they can take the species into account in their usage of the area.

For sea lamprey, the general assessment is that there is no need for confidentiality or generalisation of occurrences in the release or publication of occurrence data.

Impact and Coordination

Impact

Effects of the Action plan on different habitat types and on other Red List species

The threats to species dependent on large watercourses are mostly similar. Therefore, all measures aimed at restoring natural environments and processes in watercourses can be considered positive for a wide range of species. Aquatic species include salmon, river lamprey, freshwater pearl mussel, eel and burbot. Terrestrial species such as kingfisher and otter also benefit from improved watercourse conditions.

Among the habitat types listed in Annex 1 of the Habitats Directive, Large watercourses (3210 Fennoscandian natural rivers) and Small watercourses (3260 Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation) are the most important.

Conflicts of interest

Several of the measures proposed in the Action plan aim to reduce the negative environmental consequences of historical or ongoing exploitation of watercourses. The measures may therefore be in direct conflict with both cultural-historical values and ongoing activities in the form of power generation, water regulation, exploitation and land drainage.

Coordination

Most of the general and site-specific measures identified in the Action plan are in line with the county administrative boards' obligations under the Water Framework Directive and the action plans adopted by the water authorities. There should also be coordination with the national management plans for eel and salmon and the county administrative boards' supervision of water activities.

The National Hydropower Re-evaluation Plan “Hydropower on modern environmental terms“ should take into account the sea lamprey action programme in such a way that the power plant nearest to the sea in each catchment area is prioritised over work on upstream power plants in the same catchment area, in order to increase the area of available habitat as quickly as possible.

Suggested coordination with other action plans

The action plan for sea lamprey covers many of the same habitat types and measures as the action plans for aspen, river lamprey and freshwater pearl mussel. The action plan for eelgrass beds concerns important nursery areas for many of the sea lamprey's host fish.

Suggested coordination with environmental monitoring and follow-up other than in this Action Plan

The sea lamprey is a very good umbrella species for the larger watercourses in Västra Götaland, Halland and Skåne, due to its limited ability to cross artificial migration barriers and its requirements for a varied running water environment. Where viable populations of sea lamprey exist, conditions are expected to be favourable for other species associated with larger watercourses. A future monitoring programme for sea lamprey should therefore be coordinated with other ongoing environmental monitoring. Coordination can, for example, help to ensure that all fish species, irrespective of their capabilities to pass migration barriers, are considered within different management plans and in the development of best practice guidelines.

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Appendix 1. Proposed activities

Activity	County	Area/Vicinity	Actor	Financier	Estimated Cost (SEK)	Priority	Implemented by
Information and advice							
Short factsheet on the sea lamprey and its environmental requirements.	Halland		SwAM, County Administrative Board	SwAM-Action Plan	50 000	2	2020
Development of guidelines and basic training materials on lamprey. Species identification, ecology, inventory methodology.	Halland		SwAM, County Administrative Board	SwAM-Action Plan	50 000	2	
Information signs at known public spawning areas. Develop a non-site-specific sign template that can be used in any location.	Halland		County Administrative Board	SwAM-Action Plan	50 000	2	2020
Education							
Course in species knowledge, inventory methods, and environmental requirements for e.g. county administrative boards, local councils, water boards, consultants.	Halland	Halland	County Administrative Board	SwAM-Action Plan	100 000	1	2020
New knowledge							
Study of behaviour and survival when passing hydroelectric turbines. Recommendations for action.	Halland	Suitable objects	County Administrative Board	Research grants	Not included	2	

Studies of larval abundance in different environments and depths. How representative is the electrofishing survey?	Halland		University, County Administrative Board	SwAM-Action Plan	50 000	2	
Investigating the origin and migration patterns of Swedish sea lampreys			University	Research grants	Not included	3	
How does the recolonisation of watercourses and stretches of water that previously had migration barriers take place?	Halland	Ätran, Rolfsån, Himleån	County Administrative Board	SwAM-Action Plan	100 000	2	
Surveys							
Mapping of breeding and nursery areas by using spawning fish inventory and electrofishing for larvae.	Västra Götaland	Salmon-bearing watercourses	County Administrative Board	SwAM-Action Plan	500 000	1	2020
Mapping of breeding and nursery areas by using spawning fish inventory and electrofishing for larvae.	Skåne	Salmon-bearing watercourses	County Administrative Board	SwAM-Action Plan	250 000	1	2020
Mapping of breeding and nursery areas by using spawning fish inventory and larval electrofishing.	Halland	Salmon-bearing watercourses	County Administrative Board	SwAM-Action Plan	250 000	1	2020
Re-evaluation of existing regulations							
Review and monitoring of water activities. In cases where re-evaluation takes place, adaptation to sea lamprey should always be required.	Västra Götaland, Halland, Skåne, Blekinge				Not included		

Ensure that fish stocks have a size and age structure that sustains ecosystem functions, including through selective fishing, the establishment of no-fishing zones or marine protected areas.			SwAM, County Administrative Boards of Västra Götaland, Halland and Skåne		Not included		
Preparation of county and/or specific watercourse plans for the re-evaluation of water activities.	Västra Götaland, Halland, Skåne, Blekinge		County Administrative Board		Not included		2024
Area protection							
Management plans and decisions for protected areas where the sea lamprey occurs should be reviewed and, if necessary, revised with regard to the habitat requirements and life cycle of the sea lamprey.	Västra Götaland, Halland, Skåne, (Blekinge)		County Administrative Board	NV	Not included		Ongoing
Protect areas that are important for the sea lamprey and its life cycle.	Västra Götaland, Halland, Skåne, (Blekinge)		County Administrative Board	SwAM	Not included		2024

Direct population strengthening measures							
Initiatives to improve re-colonisation in watercourses where the species has not established five years after measures such as removal of migration barriers or habitat restoration.	Halland	Himleån	County Administrative Board	SwAM-Action Plan	75 000		2020
Restoration and creation of habitats							
Biotope conservation measures by improving spawning and nursery areas, fringe zones, re-meandering, hollows, spawning grounds, woody debris, tree planting, fencing off animals in trampling-sensitive areas, etc.	Västra Götaland, Halland, Skåne, (Blekinge)	Existing or potential occurrences	County Administrative Boards, local councils, non-profit organisations	SwAM-Action Plan, LONA, LBP, EFF, grants for management of protected areas, biological restoration of limed areas, LOVA.	1 000 000 per County during the program period	1	2024
Free migration routes and restoration of watercourse sections							
Increase knowledge for providing original spawning and nursery habitats and to ensure water flow. Ongoing according to water management and other co-operations.	Västra Götaland, Halland, Skåne, Blekinge		County Administrative Boards	SwAM-Action Plan	200 000 SEK per county to collect and provide prioritisation information.	1	2022
Monitoring							

Monitoring	Västra Götaland, Halland, Skåne	Designated watercourses	County Administrative Boards	SwAM	Not included	1	2020
Follow-up							
Follow-up of restoration	Västra Götaland, Halland, Skåne	Areas where measures have been implemented.	County Administrative Boards of Västra Götaland, Halland, Skåne	SwAM	50 000 SEK per County.	1	2024
Total estimated cost					6 425 000 SEK		

Appendix 2. National occurrence

List of watercourses where sea lampreys are found (data up to 2018; the list is compiled by the County Administrative Board of Halland together with the Swedish Species Information Centre).

WISS ID	Main catchment area	Watercourse	County	Occurrence description, 200 m = one stretch	Year/ period
024	Rickleån	Rickleån	Västerbotten	Adults observed	1965
086	Mörrumsån	Mörrumsån	Blekinge	Adults observed	2001
087	Skräbeån	Skräbeån	Skåne	Adults observed	2006
088	Helge å	Helge å	Skåne	Adults observed	The 1990s
094	Rååån	Rååån	Skåne	Adults observed	2006-2007
096	Rönne å	Rönne å	Skåne	Adults observed	2005-2017
096		Rönne å	Skåne	A possible spawnig nest observed at Västra Sönnarslöv.	2008
097	Stensån	Stensån	Skåne	Adults observed	21st century
097		Stensån	Skåne	There are 11 stretches with spawning nests from the sea to Sjöaltesjön (40 km).	2008-2018
098	Lagan	Lagan	Halland	There is 1 stretch with spawning nests from the estuary to Laholm (10 km).	2008
098		Lagan	Halland	Adults observed	21st century
098-1		Smedjeån	Halland	There are 4 stretches with spawning nests from the estuary to Ränneslöv and Menlösabäcken to Vrångarp (15 km).	2015-2018
098-1		Smedjeån	Halland	Adults observed	1970-1980
098-1		Smedjeån	Halland	Adults observed	2000-2018
098-1-1		Edenbergaån	Halland	There are 3 stretches with spawning nests from the estuary to Edenberga (10 km).	2015-2018

099	Genevadsån	Genevadsån	Halland	Adults observed	The 1960s
099		Genevadsån	Halland	There are 2 stretches with spawning nests from the estuary to Tönnersakvarn (4 km).	2008-2018
100	Fylleån	Fylleån	Halland	Adults observed	The 1940s until 2007
100		Fylleån	Halland	There are 2 stretches with spawning nests from the estuary to Fyllingekvarn (7 km).	2008-2018
101	Nissan	Nissan	Halland	Adults observed	1984
101		Nissan	Halland	Adults observed	2008
101		Nissan	Halland	There are 3 stretches with spawning nests from the estuary to Oskarsström power plant (40 km).	2015-2018
102	Suseån	Suseån	Halland	There are 2 stretches with spawning nests from the estuary to the upstream bridge at Uddaveka (6km).	2008-2018
103	Ätran	Ätran	Halland	Adults observed	The 1950s
103		Ätran	Halland	Adults observed	1956 -2007
103		Ätran	Halland	There are 9 stretches with spawning nests from the sea to Högvadsån estuary (30 km).	2008-2018
103-4		Högvadsån	Halland	There are 4 stretches with spawning nests from Högvadsån estuary to Nydala (6 km).	2008-2018
103-4-1		Stockån	Halland	There are 4 stretches with spawning nests from Stockån estuary to the Okome Sawmill Dam (2 km).	2008-2018
103/104	Tvååkersån	Tvååkersån	Halland	From the estuary up to Utteros (0.5 km), there is one stretch with spawning nests.	2015
105	Viskan	Viskan	Halland	Adults observed	1980-1990
105		Viskan	Halland	Adults observed	Before 2008
105-3		Viskan	Halland	From the sea up to Lekvad (46 km) there are 3 stretches with spawning nests.	2008-2018

105-3		Bäck	Halland	Stream from Stora Dammsjön from the Viskan estuary and 1.5 km upstream at Lunna, there is 1 stretch with spawning nests.	2015
105-3		Lillån	Halland	There are 2 stretches with spawning nests from the outlet at Viskan to Fävren (7 km).	2015-2018
105-3		Kungsätersån	Halland	From the outlet at Fävren up to Hultaberg (2 km) there is 1 section with spawning nests.	2015
105-4		Hornån	Halland	There is 1 stretch with spawning nests from the outlet of Hornån at Viskan and 1.3 km upstream.	2015
105-5		Surtan	Halland	From the outlet of the river Viskan and 100 metres upstream there is 1 stretch with spawning nests.	2018
105-5		Surtan	Halland	Adults observed	2007
105/106	Löftaån	Löftaån	Halland	From the estuary and 15 km up to Kärrets road there are 4 stretches with spawning nests.	2015-2018
106	Rolfsån	Rolfsån	Halland	From the estuary up to Hjälm (about 15 km) there are 9 stretches with spawning nests.	2015-2018
107	Kungsbackaån	Kungsbackaån	Halland	Adults observed	2007
107		Kungsbackaån	Halland	From the sea up to Alafors (about 15 km) there are 3 stretches with spawning nests.	2008-2018
107-3		Lillån	Halland	From the outflow in Kungsbackaån to Ryared upstream of Annebergssågen (about 15 km) there are 4 stretches with spawning nests.	2015-2018
108	Göta älv	Göta älv	Västra Götaland	Adults observed vid Lärje	1871-1997
108-3		Säveån	Västra Götaland	Adults observed	1997
108-3		Säveån	Västra Götaland	Adults and spawning nests observed	2018
108-4		Lärjeån	Västra Götaland	Adults observed	1957, 1997
108-6		Sköldsån	Västra Götaland	Adults observed	1990

108-10-1		Grönå	Västra Götaland	Adults observed	1980-2003
108-10-1		Forsån	Västra Götaland	Adults observed	1985
108-10-1-1		Slereboån	Västra Götaland	Adults observed	1990
108-10-1-2		Grönå/Sörån	Västra Götaland	Adults observed	1986-1990
108-14		Västerlandaån	Västra Götaland	Adults observed	1980
108-14+		Sannersbybäcken	Västra Götaland	Adults observed	2003
108/109	Anråse å	Anråse å	Västra Götaland	Adults observed	
110	Örekilsälven	Örekilsälven	Västra Götaland	Adults observed	1987-2009
110		Örekilsälven	Västra Götaland	Adults and spawning nests observed	2018
110-1		Munkedalsälven	Västra Götaland	Adults and spawning nests observed	2009
110-1		Munkedalsälven	Västra Götaland	Adults and spawning nests observed	2018
112	Enningdalsälven	Enningdalsälven	Västra Götaland	Adults observed	2009

Sea Lamprey – Swedish Action Plan

Sea Lamprey – Swedish Action Plan Linnaeus, 1758

The action plan covers measures to strengthen Swedish stocks of sea lamprey (*Petromyzon marinus*).

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